VISUAL AND NON-VISUAL BEHAVIORS OF THE RAT AFTER EARLY AND LATE POSTERIOR NEOCORTICAL LESIONS

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ABSTRACT

Several experiments investigated the nature of the visual and non-visual changes resulting from removal of the striate areas in rats. Study I evaluated the effects of neonatal lesions on several visual and non-visual behaviors. Study II investigated the reactions of striate animals to noxious stimulation, and their ability to learn a passive avoidance task. Evidence was obtained which supports the contention that removal of the cortical visual areas in mature animals interferes with visual and non-visual behaviors in a wide range of situations. Neonatal lesions allowed recovery of some visual behaviors which were lost in animals lesioned at maturity. We concluded that early lesions are less detrimental to recovery of visual function. Some of our findings were at variance with reports in the literature, and a critical evaluation and comparison of the results of our various experiments led to the conclusion that no single explanations of the differential effects of neonatal and adult removal of the cortical visual areas are possible. In explaining apparently conflicting data methodological and phylogenetic considerations were important.

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CHAPTER I

THE PROBLEM AND INTRODUCTION

I. Statement of the Problem

There is considerable evidence for subhuman animals that early brain damage is less detrimental to behavior than similar damage incurred later in life. However, few experiments have studied early lesions in the cortical sensory projection areas and their possible effects on recovery of sensory and perceptual function. With regard to vision, it is a well-established fact that destruction of the visual cortex of the mature animal results in an irreversible loss of pattern vision, as inferred from such animal's inability to learn visual pattern discriminations. Two recent studies have shown, however, that pattern vision of mature animals will remain intact if the visual cortex damage is inflicted at birth. This suggests that in very young mammals nervous tissue is sufficiently plastic to allow re-establishment of primary visual functions in other cortical or subcortical regions. So far evidence has been restricted to one species only; the cat. We feel, however, that it is important to test the generality of such findings by attempting to provide similar evidence for another species such as the rat.

Secondly, it is important to show that, in addition to normal development of pattern vision, a variety of visual and non-visual behaviors are either normally developed or selectively impaired. This can be achieved by sampling a broad spectrum of such behaviors in the same animal. Such an approach will further our understanding of the residual visual capacity of neonatally lesioned animals, as well as of the effects of such lesions in animals operated as adults. The present study is, therefore, an attempt at a more comprehensive evaluation of the effects of neonatal and adult removal of the visual cortical areas in the rat.

II. Historical Introduction

This review deals with the effects of surgical removal of posterior neocortex on the behavior of the rat and other mammals. By posterior neocortex is meant that part of cortex which includes the primary visual projection areas, also referred to as visual cortex, occipital cortex, areas 17 and striate areas. Destruction of this part of the brain is always followed by retrograde degeneration of ganglion cells in the pars dorsalis of the thalamic lateral geniculate nucleus (Lashley, 1934). The material is presented according to a) effects of the lesion on visual behavior and b) effects on other, non-visual behavior. Each of these sections is in turn subdivided into 1) effects of the lesions made in mature animals and 2) effects of the lesion when made early, in the immature animal, on adult behavior.

A. Visual Behavior after Removal of Visual Cortex

1. Lesions in mature animals. Over the last forty years a plethora of studies evaluating the effects of removal of the visual cortex has accumulated for the rat, cat, dog, and monkey. Primarily because of Lashley's work on the striate rat i.e., a rat without its striate cortex, interest and experimental work have grown rapidly in this area. Lashley (1920) showed that striate rats can learn a light-dark discrimination in the Yerkes discrimination apparatus, which proved that such animals are not completely blind. In most experiments using

this apparatus, or a modification of it, a S learns to discriminate between a light and a dark alley, a dim and a bright light, or a black and a white stimulus card. Either the light or the dark side serves as positive stimulus; errors are punished by foot shock or by withholding of food reinforcement, whereas correct choices are rewarded by food or escape from shock.

Since the initial studies of Lashley it has been demonstrated repeatedly that striate animals can learn light-dark and brightness discriminations (Lashley, 1929, 1935, 1950; Thompson, 1960; Horel, Bettinger, Royce, & Meyer, 1966 for the rat; Smith, 1937; Schilder, 1966 for the cat; Marquis, 1934, for the dog; Klüver, 1942, for the monkey). Studies using conditioning techniques further demonstrated the striate animal's ability to respond differentially to light. Marquis and Hilgard established conditioned eyelid responses to light in dogs (1936) and monkeys (1937). Wing and Smith (1942), using the dog, conditioned leg flexion to the onset of a uniform field of light, and Wing (1946) conditioned leg flexion to changes in light intensity.

By contrast, detail, form, and pattern vision are completely abolished by the operation in the rat (Lashley, 1931; Lashley & Frank, 1934). Similar findings were obtained for the cat (Smith, 1938) and the monkey (Klüver, 1937). Although losses in pattern vision are certain in these species, recent evidence suggests that it is not possible to generalize to all mammals. Snyder, Hall, and Diamond (1966) found that in the tree shrew complete resection of the striate cortex, which was followed by complete lateral geniculate degeneration, did not abolish the ability to make pattern discriminations. His Ss could differentiate between horizontal and vertical stripes, and upright and inverted triangles in a Yerkes-type discrimination apparatus. Further confirmation of these important findings is needed.

The major problems in interpreting the inability of striate animals to perform pattern discriminations, lay in a lack of knowledge of the nature of the residual visual capacity of such animals. Smith and Warkentin (1939) and Kennedy (1939) showed that striate cats were able to respond to moving patterns. Smith and Warkentin restrained striate cats in a large rotating cylinder, lined with striations the width of which could be varied. The cats' optic nystagmus was used as an indicator of visual acuity. It was found that _Ss_ responded in a manner which suggested normal minimum visual acuity. Deficiencies were only observed if the striations were widely separated. On these grounds the investigators proposed that in striate cats not all aspects of pattern vision are abolished. While one may question the validity of the assumption that optic nystagmus is a good indicator of visual acuity, and of the ability to respond to patterned visual stimulation, above all this study points to the necessity of studying a function, such as pattern vision, in different situations and tasks.

Klüver (1942) reviewed his work on the striate monkey, which is likely to be the most thorough and ingenious approach to the question of what are the sensory and perceptual changes which result from striate removal. Klüver found that the striate monkey responds to visual stimuli on the basis of differences in quantities of light energy, or differences in _luminous flux_, which he likened to the action of a photocell. For example, he showed (1941) that striate monkeys cannot differentiate between a large and a small square stimulus if the same amount of luminous flux is emitted by both, even though one of the squares may be objectively brighter than the other. Smith's research (1937) makes one suspect that the striate cat also responds on this basis. He found that such animals needed a greater number of trials to learn an intensity discrimination when the level of ambient room illumination was increased, and that the habit could not be learned with further increases of ambient illumination. Striate animals, according to Klüver, cannot localize a light source in space but respond by minimizing and maximizing flux differences by changing body, head and eye positions. In Smith's situation, Ss can maximize flux differences between the stimuli only when room illumination is low. Any increase in illumination is an addition of luminous flux which reduces discriminability between the stimuli. That cats respond on the basis of luminous flux has recently been shown by Schilder (1966). Bauer & Cooper (1964) presented similar evidence for the rat.

Changes resulting from striate removal, from normal vision to a sensitivity to luminous flux, affect not only spatial vision, pattern vision, or certain aspects of it, but probably all aspects of visual perception. A task, which involves a brightness discrimination for a normal animal involves a discrimination between stimuli differing in luminous flux for the operated animal, despite the finding that there may not be any differences in learning of the task (Lashley, 1935). The puzzling observations that striate area removal always results in the loss of a preoperatively established brightness discrimination (Lashley, 1935; Marquis, 1934; Thompson, 1960, Fishman & Meikle Jr., 1965) can be explained on the basis of Klüver's analysis. Rather than interpreting such data as losses of memory or engrams, it can be suggested that disturbances in learned behavior occur because of changes in the stimulus conditions, as a result of the operation. Support for this was obtained by Bauer and Cooper (1964) and Horel et al. (1966).

The effects of striate cortex lesions on other visual behaviors have been studied. Altman (1962b) showed that striate rats showed decreased light aversion when compared to normal rats. This contrasts with earlier findings by Abelman and Morgan (1943) who found increases in light aversion resulting from the operation. However, apart from differences in testing procedure, Abelman's rats had smaller lesions, and the two studies are, therefore, not really comparable. Visual cliff behavior in rats and cats was investigated by Meyer, Anderson, and Braun (1966). They found that rats behaved like enucleated animals in that their preferences for the deep and shallow sides of the cliff were not different. Cats, on the other hand, responded like normal animals in that they preferred the shallow side of the cliff. Three out of four cats showed incomplete geniculate degeneration, although the one subject, in which degeneration was complete, still preferred the shallow side 87.5% of the time. The authors account for their findings in terms of differences in postoperative environments; rats were kept in restricted colony cages, while the cats were kept in an enriched environment. The possibility is considered, however, that these differences could have been species specific characteristics.

2. Effects of early removals. Several studies have shown that early lesions of sensory cortical areas allow recovery of some functions which are lost after similar removals in adult animals. Benjamin and Thompson (1959) showed that early removals of somatosensory areas of the cat's cortex did not impair simple roughness discriminations,

although impairments were found when the task was increased in difficulty. Scharlock, Tucker, and Strominger (1963) reported neonatal removal of the auditory projection areas in the cat which did not abolish the ability to discriminate auditory patterns, whereas such ability was abolished when the operation was done in mature animals. It is possible that in early lesioned animals the nervous system is sufficiently plastic to allow structural reorganization to occur, so that other areas of the brain become responsible for pattern and form vision. Such an explanation is congruent with the behavioral data and cannot be ruled out by such findings as presented by Hubel and Wiesel (1963), who observed that electrical responses and receptive fields are organized normally in the 1-week old kitten.

There is at present no corresponding evidence for the rat. However, Tsang (1937) reported that early lesioned Ss may retain some pattern vision. Visual areas were removed in 22-days old rats and 4/10 animals showed differential reactions to visual patterns. Cajal (1960) has shown that the cortex of the mouse is functionally mature only at about 8 to 10 days after birth. Therefore, lesions made prior to this time may not be as detrimental to recovery of function because of possible structural changes. Such changes might also occur in the rat, as well as in the cat. Which structures become involved in pattern vision in early lesioned animals is not known. Doty (1961) favoured the notion that other cortical areas are involved. On the other hand, it is just as likely that subcortical structures are important. As the superior colliculi are homologous to the optic lobes in primitive animals it is possible that they could subserve pattern vision in neonatally lesioned animals. Evidence exists which shows that even in normal animals these structures play an important role in complex visual behavior (Blake, 1959; Sprague & Meikle, 1965).

B. Non-Visual Behaviors after Striate Area Removal

1. Lesions in mature animals. A number of investigators have reported impaired learning of various learning tasks as a result of posterior cortex removal. In a well-controlled study by Tsang (1936) visual areas were removed in rats that had been blinded at birth. Learning of both an open and enclosed maze was retarded. Tsang suggested that, in addition to being necessary for normal visual behavior, the visual cortex has a general facilitating function in learning. His findings were supported by those of Lashley (1943). Learning impairments were also reported by Landsdell (1953) who tested posterior rats in a Hebb-Williams maze.

Other types of learning have been studied. Krechevsky (1936) reported that lesioned rats had great difficulty in learning a brightness discrimination reversal habit. Lubar, Schostal, and Perachio (1967)found that postoperative learning of an active avoidance response was impaired in the cat. His *Ss* were required to escape foot shock by jumping across a hurdle in a two-way avoidance apparatus. Posterior *Ss* took significantly more trials to learn this than normals. These studies point to a non-visual function of the striate cortex, and there seems no doubt that in addition to it's importance in sensory function, this part of the brain is somehow important in learning.

2. Effects of early removals. On the basis of evidence obtained from the human literature Hebb (1949) proposed that infant brain lesions are more deliterious to complex intellectual function than adult brain damage. An exception to this are cases where the damage

involved the speech areas. Roberts (1958) reported that in contrast to patients who incurred such damage as adults, similar lesions in children younger than 2 years of age will not always result in aphasia. Evidence obtained for lower animals suggests that 'intelligent' behavior is less impaired by early lesions. Landsdell (1953) removed anterior and posterior cortices in 18-20 and 74-76 days old rats and studied their performance on 24 problems in the Hebb-Williams maze. Early posterior Ss showed less impairment than later lesioned Ss, whereas no such differences were seen between performance of corresponding anterior groups. Smith (1959), however, found no differences in Hebb-Williams maze learning in rats who had small posterior cortex lesions, outside the visual cortex, at 20 to 25 and 95 to 100 days of age. The lesion effect, independent of the age of operation, was found to depend on the complexity of the environment in which Ss had been reared. Schwartz (1964) found that an enriched postoperative environment would offset the effects of posterior, visual cortex lesions received at one day of age. However, none of the rats had lesions which involved the whole visual cortex and the study lacked a later lesioned control group for comparison.

From this review of the literature several conclusions can be drawn. Striate lesions in adult animals will abolish visual pattern discrimination and leave intact only an ability to respond to visual stimuli on the basis of luminous flux cues. However, according to Klüver (1942):

> "results obtained on various animals lacking the visual cortex have often led to the interpretation that the operation abolishes or seriously disturbs certain visual functions, such as spatial orientation, while it leaves other functions, such as brightness vision intact. As far as the monkey is concerned, it is more correct to say that all aspects of vision are affected by the operation and that none of the functions remains normal".[1]

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[1] Klüver, H. Functional significance of the geniculo-striate system. p. 278-279.

A review of the various experiments in the literature tends to support this conclusion. Impairments in non-visual behaviors suggest, moreover, that the visual cortex is involved in more than just visual behaviors and has some complex integrating function. The possibility that early lesions will not abolish pattern vision needs to be investigated further. If early lesions allow recovery of pattern vision, then a similar recovery of other aspects of vision, as tested in different tasks, is likely to occur. To study and to explain the behavior of early and late lesioned rats is the object of the studies reported in the following chapters.

CHAPTER II

STUDY I

The Problem

Traditionally, removal of neocortical sensory areas has been found to result in different types of deficits: specific sensory and perceptual, and non-specific and non-sensory. In terms of these categories the present study attempts to evaluate the behavior of animals in which the visual or striate areas have been removed. One of our aims is to obtain a broader view of the nature of the residual sensory, perceptual capacity of early and late lesioned striate rats by studying a variety of visual behaviors.

Removal of the cortical visual areas in the neonate cat does not abolish pattern vision as it does when made in the adult animal. As the rat has been used in the greater number of biopsychological experiments studying visual behavior, it is important to demonstrate whether a similar recovery of pattern vision will occur in this animal. So far, striate area removals, performed mainly in adult animals, were found to abolish form, detail, and brightness vision, and leave intact only a primitive sensitivity to luminous flux, or total amount of light entering the eye. A more specific objective of this study is to discover whether detail vision can be retained in neonatally lesioned rats.

In ascribing deficits to a particular lesion it is important to minimize the possibility that a particular performance deficit could have occurred because of motivation or learning capacity. Although it is not possible to separate unequivocally sensory and non-sensory deficits, we hope, by studying a variety of non-sensory effects on behavior of early operated striate rats, to obtain greater insight into the various effects of such lesions, so that more sensible and more specific interpretations can be made.

GENERAL METHOD

Subjects

Twelve hooded pregnant rats of the Royal Victoria Hospital strain were obtained from the Quebec Breeding Farms. Ss were housed in single cages and had free access to water and fox-chow pellets. The young were delivered within 14 to 15 days after arrival. Except for one S who killed and devoured her litter, all births were normal. Litters ranged from 2 to 13 and the average was 7 young. Ss were assigned randomly to the experimental groups and the type of operation was constant for all Ss within a litter. All Ss were operated on twice, first at one day of age and again as adults. By this method the following groups of male subjects were obtained:

Group	1st Operation Neonatal Lesion	2nd Operation Adult Lesion	Number Surviving
AS	Anterior Cortex	Sham	7
PS	Posterior Cortex	Sham	11
SP	Sham	Posterior Cortex	8
SS	Sham	Sham	10

Surgery

Neonatal surgery was performed within 12 to 14 hours after birth. At this time half of a litter was removed and placed in a small cardboard box containing gauze, covered with Celluwipes. Ss were kept warm by a 60-w bulb in a desk lamp about 12 in. above the box. The same operation was performed on all Ss within a litter. After surgery Ss were returned to the mother. The other half of the litter was then operated. At all times there were some young in the nest.

Anesthesia and surgery were administered in a fashion similar to that outlined by Schwartz (1964). A 3.5 x 3.5 x 1.5 in. plastic container was filled with crushed ice. To induce hypothermia a S was wrapped in soft plastic, placed on ice and restrained until it became immobile. For the operation, the S's head was fitted through an opening in a cardboard surface, which in turn was placed over the plastic box.

After midline incision and retraction of skin the skull was punctured on either side of the midline by a 25 ga. hypodermic needle. Beginning at the punctures, the skull was cut with very fine scissors in order to produce two laterally-hinged bone flaps. For posterior operations the flaps covered the dorsal surface between bregma and lambda while for anterior operations it covered the area between bregma and the tip of the frontal portion of the skull. After retraction of the bone flaps, lesions were produced by suction through a finely drawn pipette, with a tip opening of 1 mm. The same procedure was used for sham operations, except that no tissue was removed. After removal of tissue the flaps were folded back into position, and the wound was sutured, using one fine strand of surgical thread. Ss were placed back in the warm storage box for about 15 min. after anesthesia had worn off, as indicated by limb movement and vocalization. To prevent the mother from licking the wound the skull was painted with a weak solution of quinone before Ss were returned to the nest.

At 50 days of age the second operation was performed. Striate cortex removals and sham operations were made under ether anaesthesia, with the Ss immobilized in a Stoelting stereotaxic holder, using earplugs and incisor bars to fasten the head. With dental burrs the skull was removed dorsally from 1 to 2 mm. behind bregma, rostrally to lambda, leaving a ridge of bone of 1 to 2 mm. along the midline. The exposed cortex was removed by suction. In the controls the dura mater was pierced without removing any tissue. Half of the previously sham operated Ss received posterior neocortical lesions, while all other animals were sham operated. Anterior Ss received posterior sham operations while previously posterior lesioned Ss received anterior sham operations. This was done in order not to interfere with the healed site of the previous operation. At the end of the experiment Ss' eyes were dilated with Mydriacyl (Tropicamide .5%) and examined by an ophthalmologist. Ss were then killed with ether and their brains perfused with saline and 10% formalin. Brains were sectioned and the tissue stained, using the method outlined by Klüver and Barrera (1953). From the slides, the size and extent of the lesions were reconstructed on Lashley-type diagrams.

Procedure

At 21 days of age Ss were separated from their mothers, and males only transferred to colony cages (24 x 24 x 18 in.). At 50 days of age, after the second operation, Ss were transferred in pairs to smaller cages (8 x 7 x 9.5 in.). At all times Ss had free access to water and Purina fox-chow pellets. Dark and light periods in the animal room were 12 hours each and automatically controlled; lights came on at 8 A.M. and were turned off at 8 P.M. The following tests were given before the second operation:

Visual Cliff (I)
Light Preference (I)
Activity (I)

Two weeks after the second operation these tests were repeated and further studies were made, in the sequence outlined below:

Visual Cliff (II)
Light Preference (II)
Activity (II)
Brightness Discrimination
Pattern Discrimination
Brightness Discrimination Retraining and Reversals
Brightness Discrimination under different Levels of Illumination
Response to Depth from a Raised Platform

These experiments will now be discussed in detail.

EXPERIMENT I

VISUAL CLIFF

The Problem

The various effects resulting from removal of the striate areas in mammals were summarized by Klüver (1942) when he stated:

> "the elimination of the geniculo-striate system leads to a complete or a practically complete elimination of visuo-spatial properties as effective determinants of behavior or, more briefly, to an elimination of visual space with its dimensions".[2]

The visual cliff apparatus (Gibson & Walk, 1960) is a useful tool to assess the ability to perceive and respond to visual depth in a great variety of animals (Shinkman, 1962; Routtenberg, 1964a, b; Walk, 1965). As striate removal abolishes form and pattern vision one would expect it to interfere with visual cliff behavior. While striate cats

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[2] Klüver, H. Functional significance of the geniculo-striate system, p. 278.

seem to be able to respond to the visual cliff (Meyer, 1963; Meyer, Anderson, & Braun, 1966) the evidence for the rat suggests that the response is abolished after such lesions (Meyer et al., 1966). As a test of the hypothesis, that neonatal removal of visual areas of the rat will not interfere with development of normal visual cliff behavior, the present experiment was performed.

Method

In addition to the four groups described in the previous section, AS (N = 7), PS (N = 11), SP (N = 8), SS (N = 10), a group of Albinos (N = 10) of the Holtzman strain was used as an extra control for the Visual Cliff Test (I).

Apparatus

The visual cliff was constructed from an open field, 32 x 32 x 9.5 in., which was suspended in a wooden frame 26 in. above the floor. Half of the area was covered by red and white (1/4 in.) checkered, vynyl coated, translucent paper placed in between two glass plates which were of the same size as the field. The same patterned paper covered a third glass plate 15 in. below, and constituted the deep side of the cliff. The field was separated into halves by a 3.5 x 3.5 x 32 in. center board, covered by the same material, which also covered the walls of the apparatus. In order to eliminate reflection, the apparatus was illuminated from below. Attempts were made to have equal amounts of illumination on each side of the center board.

Procedure

Each S was placed on the center board for a 5-minute period and the number of entries into the deep and shallow side were recorded. Boli were removed immediately, and after each animal the centerboard and the glass floor were wiped with a moist cloth. All observations were made from a position in line with the center board.

Results

Table I indicates that, during the first visual cliff performance test, anteriors and shams clearly preferred the shallow side of the cliff, as indicated by their first responses, in contrast to the performance of the albinos. While posterior animals have a tendency to prefer the shallow side, this preference is obscured by the fact that 4 out of 11 Ss did not leave the center board. If only those Ss are considered which in fact did leave the center board (Table II) it can be seen that all Ss did prefer the shallow side. For the second test, Visual Cliff II, performed after the second operation, most groups preferred the shallow side, with the exception of the late posteriors, who showed no particular preference for either side.

TABLE I

FIRST RESPONSES TO DEEP AND SHALLOW SIDES OF VISUAL CLIFF. OF ALL SUBJECTS

	N	Shallow Responses	Deep Responses	Inhibited Responses
VISUAL CLIFF I		%	%	%
Anteriors	7	86	0	14
Posteriors	11	64	0	36
Shams (1)	8	100	0	0
Shams (2)	10	90	10	0
Albinos	10	50	40	10
VISUAL CLIFF II				
Anterior-Shams	7	86	14	0
Posterior-Shams	11	82	9	9
Sham-Posteriors	8	50	50	0
Sham-Sham	10	100	0	0

TABLE II

FIRST ENTRIES INTO DEEP OR SHALLOW SIDES OF VISUAL CLIFF OF SUBJECTS WHICH DESCENDED

	Shallow Side	Deep Side
VISUAL CLIFF I		
Anteriors	6	0
Posteriors	7	0
Shams (1)	8	0
Shams (2)	9	1
Albinos	5	4
VISUAL CLIFF II		
Anterior-Shams	6	1
Posterior-Shams	9	1
Sham-Posteriors	4	4
Sham-Shams	10	0

When the total number of responses during the 5-min. test period are analyzed (Table III) a similar picture emerges. During Visual Cliff I all _Ss_, except the albinos, made a greater number of

TABLE III

TOTAL ENTRIES INTO DEEP AND SHALLOW SIDES OF VISUAL CLIFF

	N	Shallow	Deep	Difference	Mean Difference
VISUAL CLIFF I					
Anteriors	6	18	0	18	3.00
Posteriors	7	28	7	21	3.00
Shams (1)	8	36	2	34	4.25
Shams (2)	10	32	6	28	2.80
Albinos	10	66	61	5	.50
VISUAL CLIFF II					
Anterior-Shams	7	28	10	18	2.57
Posterior-Shams	10	38	14	24	2.40
Sham-Posteriors	8	31	25	6	.75
Sham-Shams	10	33	5	28	2.80

entries into the shallow than into the deep side. Similarly, all Ss except the late posteriors (SP) showed a preference for the shallow side during the second test (Visual Cliff II). A Mann Whitney U test was made on the difference scores between PS and SP groups and found to be significant ($U = 14.5$, $p < .025$ [2-tailed]).

Discussion

The results agree with those of Routtenberg (1964a) who reported that albinos responded randomly in the visual cliff situation, as well as those of Meyer (1966), who found that the normal visual cliff response was abolished in striate rats. The most important finding of the present experiment is that neonatally lesioned striate rats do not lose the visual cliff response, and that their performance improves with experience, as can be seen in comparison between visual cliff tests I and II. The behavior of 4 out of the 11 posterior animals in visual cliff I is difficult to interpret. Walk (1965) showed that the number of "no descents" increased with an increase in task difficulty. Applied to the present data it might mean that early lesioned animals have a deficit which is overcome on the second presentation of the task. However, such interpretation is questionable if one considers that of the late posteriors, for which the task seems most difficult, there were no Ss which did not descend. While we do not know the reason why some of the Ss did not descend during visual cliff I, it seems certain that early lesioned striate rats will respond to a visual cliff like normal animals. We feel, therefore, the hypothesis that neonatally lesioned Ss will develop normal visual cliff behavior has been confirmed. Whether this applies also to other types of visual behaviors, as measured by different tasks, will be investigated in subsequent experiments.

EXPERIMENT II

LIGHT PREFERENCE

The Problem

Rodent's reaction to light has been a topic of considerable interest in recent literature. Among the many variables which will effect a rat's response to light are light intensity, genetic factors, and maintenance history (Lockard, 1963). The general evidence supports the contention that normally rats will avoid bright lights, and, therefore, can be said to show light aversion. This aversion can be modified, increased, or decreased by lesions of CNS structures involved in vision. Abelman and Morgan (1943) showed that striate rats show increased light aversion. By contrast, Altman (1962) reported that lesions anywhere in the visual system will decrease, but not abolish, light aversion. On the other hand, Krechevsky (1936) reported that his rats would show a complete reversal in preference after the operation, i.e., striate rats will seek the brighter of two stimuli. There are procedural as well as strain differences between the various studies. For example, in the Abelman and Morgan study Albino _S_s could turn off a light by bar pressing, and the lesions were small, while in Altman's study hooded _S_s were placed in an open field having access to light and dark alleys. Knowledge of such changes in light aversion as a result of brain lesions is important if one wishes to evaluate animals' visual behavior as, for example, in a brightness discrimination task where _S_s are required to run either toward or away from a bright alley or stimulus. With this in mind, the present study was designed to test the hypothesis that striate rats would show at least a decrease in light aversion.

Secondly, we wished to discover whether the age at which the lesion was made would affect the resultant changes in light aversion.

Method

Apparatus

A wooden runway, 72 x 7 x 7.5 in. was used. Half of it was illuminated by a 25 watt bulb in a desk lamp 11 in. above. The floor was painted black while the walls had a natural light colour. A Brockwell lightmeter, model S, was used to obtain measurements of amount of light in foot candles, every 12 in. throughout the length of the runway and gave the following readings: 2, 4, 8, 24, 56, 96 ft- c.

Procedure

Each S was placed in the middle of the runway, facing the light, and allowed to explore for a five-minute period. E made his observations from a point in line with the middle of the runway and noted the times spent by the Ss in each half of the apparatus, i.e., the light and dark halves.

Results

The Ss' preferences for the high and low illuminated parts of the apparatus are shown in Fig. 1 in terms of mean time spent in the dark minus time spent in the light. The 0-line indicates the point at which equal amounts of time were spent in either side; a plus score that more time was spent in the dark; a minus score that more time was spent in the light. It can be seen that for test I the early posteriors (P) spent a longer period in the light than all other groups. Table IV shows the means and results of statistical tests.

The results are similar for test II except that the previous sham group, which underwent posterior cortex removals, showed a significant change towards spending more time in the light and now differed significantly from all other groups. Means and results of tests are presented in Table V.

TABLE IV

LIGHT PREFERENCE TEST I

MEAN TIMES IN SECONDS SPENT IN DARK MINUS TIME SPENT IN LIGHT AND RESULTS OF STATISTICAL TESTS

	Anteriors	Posteriors	Shams (1)	Shams (2)
Means	38.00	18.80	30.50	39.40
Mann Whitney U test	Posteriors vs. Shams (1) : U = 20.5, p < .05 1-tailed Shams (1) vs. Shams (2) : U = 27.5, p > .05 2-tailed			

TABLE V

LIGHT PREFERENCE TEST II

MEAN TIME IN SECONDS SPENT IN DARK MINUS TIME SPENT IN LIGHT AND RESULTS OF STATISTICAL TESTS

	AS	PS	SP	SS
Means	38.40	14.00	2.15	26.40
Mann Whitney U test	PS vs. AS : U = 12, p < .01 2-tailed PS vs. SP : U = 22.5, p < .05 1-tailed PS vs. SS : U = 35.5, p > .05 2-tailed SP vs. SS : U = 11, p < .01 2-tailed AS vs. SS : U = 31, p > .10 2-tailed			

Comparison of the post-operative performance of the late lesioned group (SP) with that of the early lesioned group (P) shows that SP animals spent significantly more time in the light (SP Mean = 2.15, P Mean =

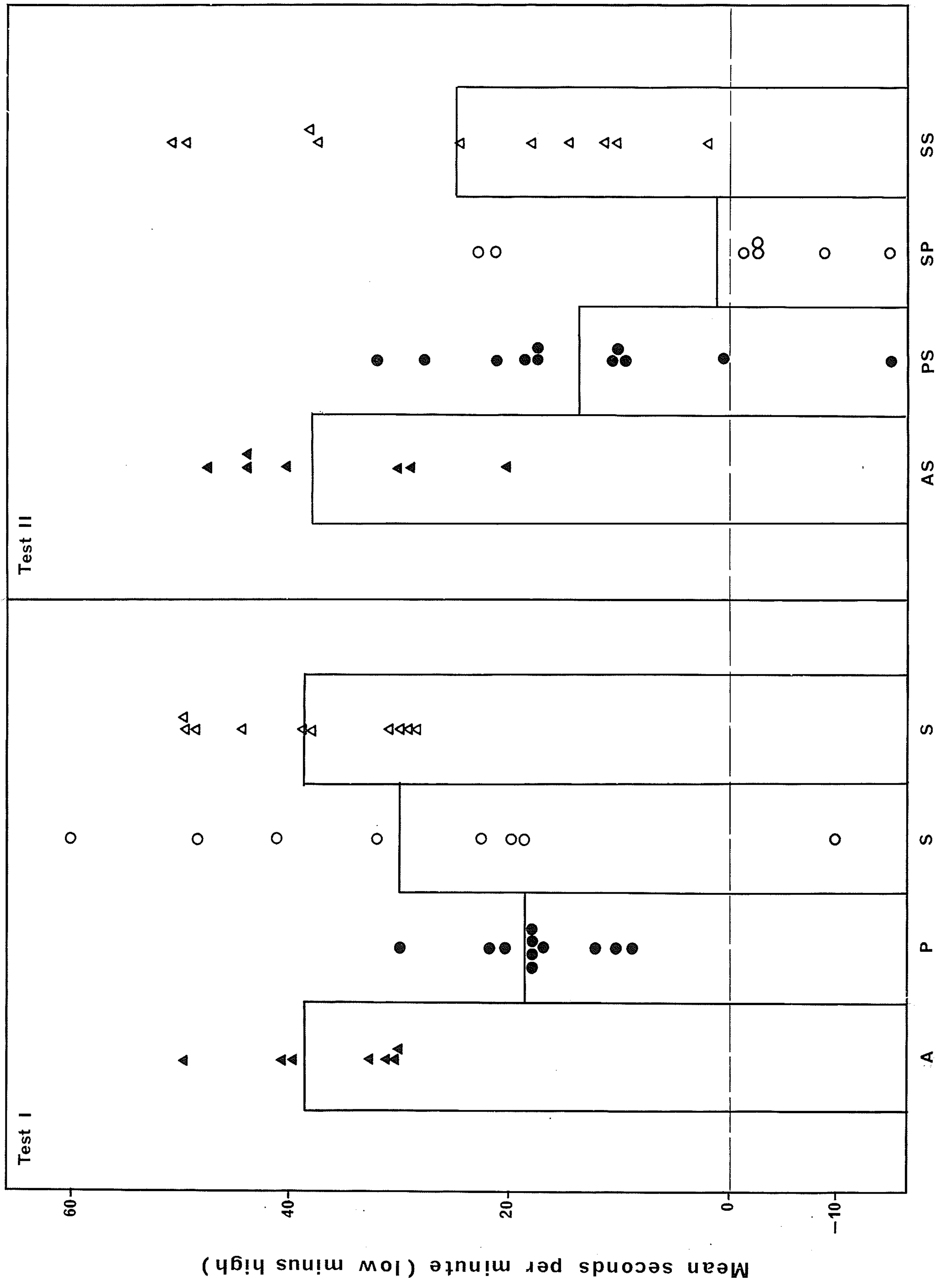
Test I
Test II
Mean seconds per minute (low minus high)
60
40
20
0
−10
A
P
S
S
AS
PS
SP
SS
Illumination preference

Figure 1.

18.80 seconds, $U = 19$, $P = .05$ /2-tailed/). Comparison of SP with their own performance prior to the operations (S_1) showed significant change towards longer time spent in the light postoperatively (SP Mean = 2.15, S_1 Mean = 30.50 seconds, $p < .01$ /2-tailed/), (Wilcoxon Matched Pairs Signed Ranks Test). The differences between S_2 and SS were not statistically significant.

Discussion

These experiments demonstrate decreases in light aversion after removal of the cortical visual areas similar to those found previously by Altman (1962). Differences in the degree of reduction of aversion are apparent between early and late lesioned _S_s. There was little change in the scores of early lesioned anterior and posterior groups from the first to the second test, which suggests that under the conditions of these experiments the effect is relatively stable. Furthermore, the change in the late posterior group's performance, as well as the absolute level of performance, supports the conclusion that removal of the visual areas in the adult animal results in a greater decrease in light aversion, than when lesions are made early in life. On the other hand, the performance of the PS group forces us to conclude that, while the time of lesion is important with regard to the degree of change in light aversion, the lesion itself has an effect independent of the age variable.

EXPERIMENT III

BRIGHTNESS DISCRIMINATION

The Problem

Lashley (1920, 1929, 1935, 1950) had demonstrated repeatedly, that although a previously learned brightness discrimination is lost as a result of striate removal, it can be relearned with the same number of trials and errors as in original learning. He also showed that there are no differences in initial learning of the habit between striate and normal rats (1929, 1935). If one considers that to the striate S a brightness discrimination is a discrimination between luminous fluxes (Klüver, 1942; Bauer & Cooper, 1964; Goodall & Cooper, 1965; Schilder, 1966) it is surprising that performance on what are essentially different tasks, i.e., a brightness discrimination for normal, a luminous discrimination for striate rats, should be exactly alike. Recent experiments (Bauer & Cooper, 1964; Horel et al., 1966) have questioned these early findings. Horel argued that differences in rates of relearning are obscured by greater light aversion shown by normal rats. Similar arguments have been applied to explain equal rates of original learning by normal and striate rats (Krechevsky, 1936). Apart from a study by Marquis (1934), who reported differences in initial learning of a brightness discrimination between normal and striate dogs, few data are available on original learning rates. No recent data can be found for the rat. The present experiment was performed to determine if a) differences in original learning between striate and normal rats could be found and b) whether the age of the animal at the time of operation is an important variable.

Method

Apparatus

A modified Yerkes-type discrimination apparatus was used (Fig. 2). The independently operated light sources were two 100-w General Electric light bulbs. The outside of the box was painted black and the inside dark grey. For discrimination training 5 x 5 x 1/8 in. translu-

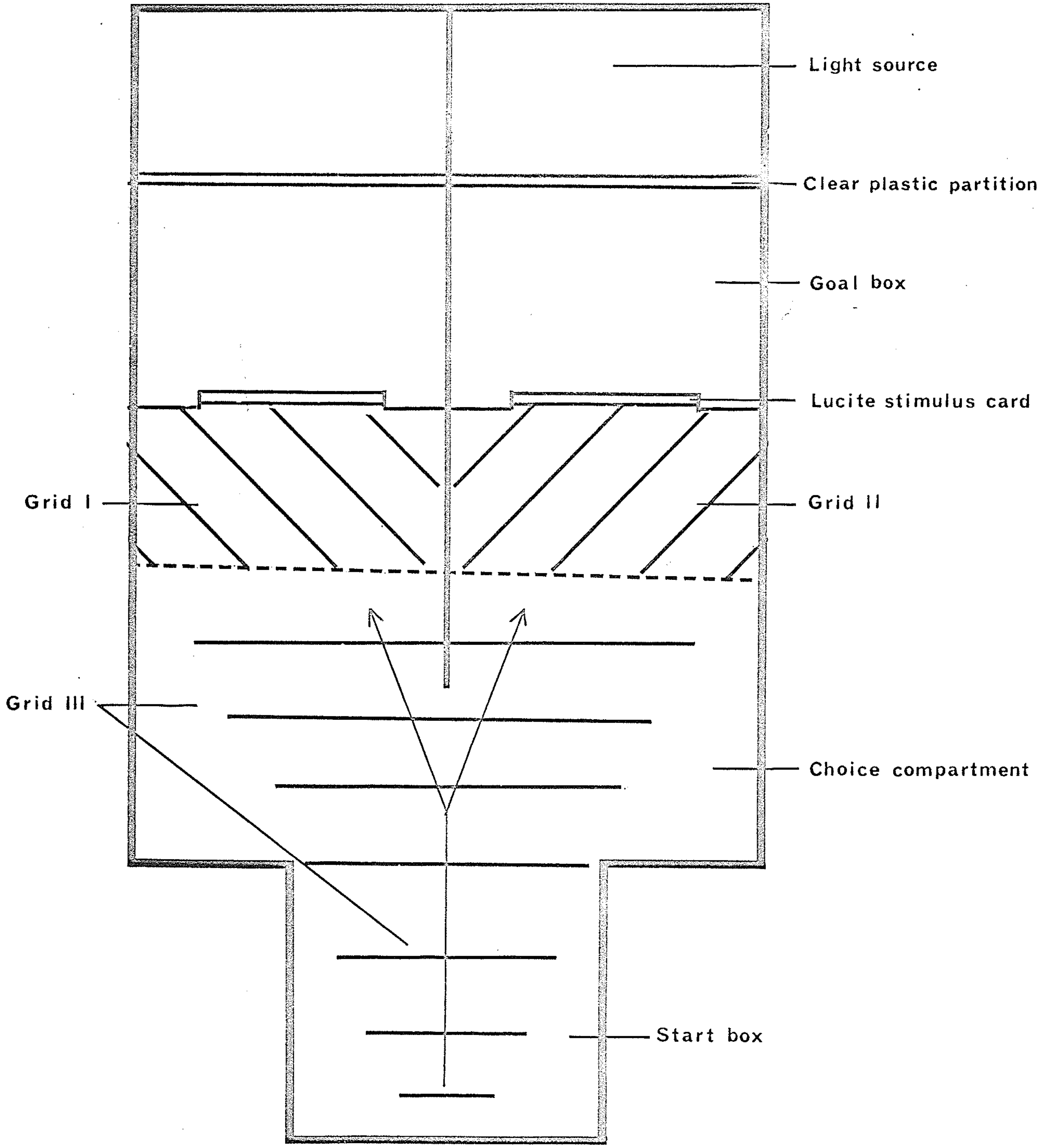

Figure 2. Discrimination apparatus

cent Lucite stimulus cards were placed against the 4 x 4 in. opening of the 1/2 in. thick partition that separated choice and goal compartments. Electric current could be supplied independently to grids I, II, and III, from a variable shock source set at 1 ma.

Procedure

On day 1 Ss were put, two at a time, into the start chamber and allowed to explore the apparatus for 15 minutes. The following day shock avoidance training was given. Ss learned to leave the start box within 15 seconds in order to avoid 1/5 second foot shock. Further shocks were given every 5 seconds until S had entered the goal chamber, after which the light on that particular side was turned off for a 10 sec. intertrial interval. Training was continued until a criterion of three consecutive shock free trials had been reached. On the following two days training was continued except that two white S cards were gradually, over three trials, moved across the goalbox opening until it was covered completely. Ss had to learn to push the card over and step into the goal compartment for 3 consecutive trials, on each of the two days, without receiving any foot shock. This was followed by 10 daily trials of brightness discrimination with the white card as the positive, and a black opaque card as the negative stimulus. Stimuli were switched from side to side according to a different Gellerman series every day (Hilgard, 1958) with the grid being continually charged in front of the negative card. S was considered to have made an error as soon as it entered the incorrect side far enough to receive a foot shock. Training was discontinued after Ss had reached a criterion of 18/20 errorless trials within two consecutive days.

Results

The first part of Fig. 3 shows errors to criterion for the various individuals and groups. It is apparent that the majority of Ss from both posterior groups made more errors in learning the brightness discrimination than those of the two control groups. This is brought out more clearly by Table VI which shows both mean errors and trials to criterion. The two posterior groups had significantly more mean errors than the controls. A one-way analysis of variance made of the transformed errors (square-root transformation) yielded an overall F of 15.87 which is significant at $p < .001$. It is clear from the table that there were no differences between early and late lesioned posterior groups.

TABLE VI

BRIGHTNESS DISCRIMINATION LEARNING
ERRORS AND TRIALS TO CRITERION

	AS (N = 7)	PS (N = 9)	SP (N = 6)	SS (N = 10)
ERRORS				
Total	34	73	57	29
Mean	4.85	8.11	9.50	2.90
TRIALS				
Total	220	350	280	270
Mean	31.40	38.90	46.70	27.00

Discussion

In contrast to the results for the visual cliff experiment the present data show that early and late lesioned striate rats are equally impaired in learning a brightness discrimination. This is surprising as it suggests a permanent deficit in performance on a relatively simple

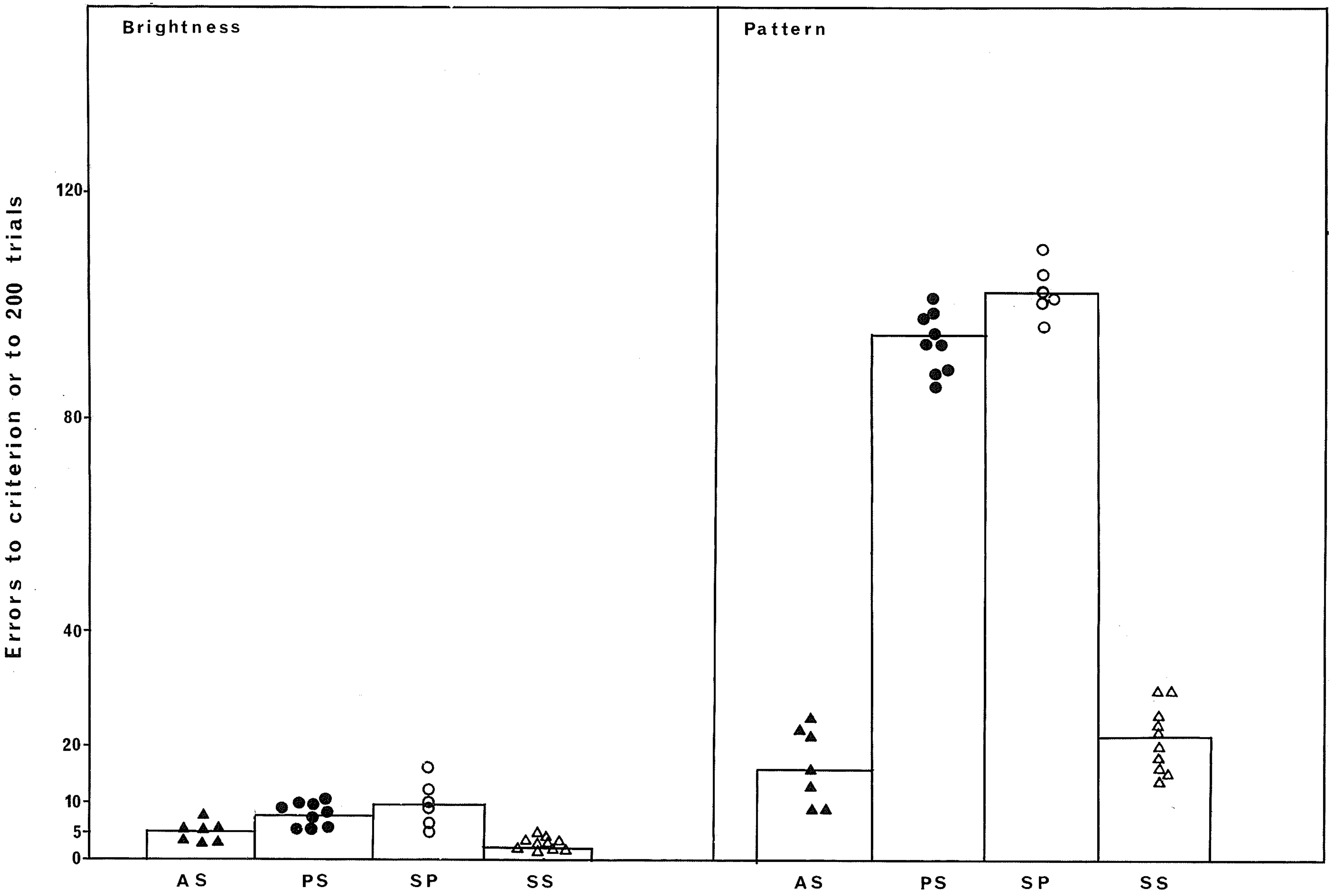

Figure 3. **Discrimination learning**

visual task, independent of the age of surgery. Furthermore, these findings are in disagreement with those of Lashley (1929, 1935) while they confirm those of Marquis (1934) and unpublished observations by Cooper (1967).[3] That these deficits could have been brought about by differences in light aversion between normal and striate rats is ruled out by the results of Experiment II. If anything, the posterior animals, having a smaller degree of light aversion than the controls, should have shown a better performance than the control animals. We have to conclude, therefore, that brightness discrimination learning, which is a flux discrimination for striate rats, is impaired by removal of the visual areas independent of the age of the animal at the time of operation.

EXPERIMENT IV

PATTERN DISCRIMINATION

The Problem

The studies of Lashley (1930, 1934, 1939; Lashley & Frank, 1934) which showed that pattern vision in the rat depends on a minimal amount of striate cortex, as inferred from the inability of striate animals to discriminate patterns and forms, have exclusively used mature animals. The only suggestion that pattern vision is possible after complete striate removal comes from a study by Tsang (1937). His striate rats were only 22 days old at the time of surgery and were in some cases (4/10 animals) found to respond differentially to patterns. Recently, Doty (1961) reported experiments in which striate areas were removed in 2-day old kittens. A substantial number of Ss which, after histological

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[3] Personal communication, July, 1967.

analysis, were found to lack completely the geniculo striate system, had been able to discriminate visual forms and patterns as adults. Similar results were reported by Wetzel et al. (1965) except that removal of the visual areas was incomplete. As there is at present no corresponding evidence for the rat the following experiment was done to determine whether similar effects could be found for neonatally lesioned animals.

Method

Apparatus

A modified Yerkes discrimination apparatus as described previously (Fig. 2) was used. Stimulus cards were made of white Lucite and had 1/2 in. black vertical and horizontal striations.

Procedure

As soon as Ss had reached criterion on the previously discussed brightness discrimination, training on a pattern discrimination was begun. Ten daily trials were given with the horizontal stripes as positive and the vertical stripes as negative stimuli, until a criterion of 18/20 errorless trials or a total of 200 trials had been reached. As in the brightness discrimination, a new Gellerman series was used every day and Ss were trained according to a correction procedure.

Results

The results of this experiment are summarized in Table VII and the second part of Fig. 3. Fig. 3 shows that the majority of the control Ss learned the task with little difficulty and that there were no differences between anteriors and shams. By contrast not a single S of either posterior group was capable of learning the task within 200 trials.

TABLE VII

PATTERN DISCRIMINATION LEARNING
ERRORS AND TRIALS TO CRITERION

	AS (N = 7)	PS (N = 9)	SP (N = 6)	SS (N = 10)
ERRORS				
Total	116	838	609	221
Means	16.50	93.10	101.50	22.10
TRIALS				
Total	440	1800	1200	690
Means	62.85	200.00	200.00	69.00

Discussion

The present results are at variance with those reported by Doty and Wetzel for the cat. For an explanation one might be tempted to refer to phylogenetic differences. It should be recalled that differences between cat and rat were also observed by Meyer (1963, 1966) on the visual cliff. Yet, on phylogenetic grounds, one would have expected the reverse; namely the rat, being the lower animal, should have been more likely to recover pattern vision than the cat. Therefore, until further evidence is obtained, it seems prudent to avoid such interpretation. The ability of striate cats to perform in a pattern discrimination in the Wetzel study could have been due to incompleteness of the lesions. Procedural differences may account for the differences between our and Doty's study. Out of his 200 operated kittens 24 survived and were then reared at home. It is likely that this 'enriched environment' could have been the crucial factor in making pattern discrimination possible in the adult striate animal.

On the basis of the present results we must conclude, however, that pattern vision, as tested in the Yerkes discrimination situation, is lost in striate rats regardless of the age at which lesions are made. Future investigation may show whether neonatal striate removal, in combination with an enriched early environment, will make recovery of this visual function possible.

EXPERIMENT V

BRIGHTNESS DISCRIMINATION UNDER DIFFERENT LEVELS OF ILLUMINATION

The Problem

The experiments discussed so far demonstrated that early lesioned striate rats can perform normally in a visual cliff situation, are impaired in original learning of a brightness discrimination, and are incapable of learning a pattern discrimination. The visual cliff data indicate that early lesioned rats probably perceive more than just differences in luminous flux, whereas brightness and pattern discrimination data show that early and late lesioned *S*s have severe sensory losses.

Experiments by Smith (1937) and Cooper and Bauer (1964) on the cat and the rat demonstrate that light-dark discrimination is extremely labile in striate animals and easily disturbed by changes in the stimulus conditions, as for example, by changes in the level of extraneous illumination. The present experiment was designed to find out whether neonatally lesioned rats respond in a similar fashion to changes in illumination during brightness discrimination.

Method

Apparatus

The apparatus was the same as used in the previous experiment. In addition to the stimulus lights behind the black and white stimulus cards, a lamp containing a 200 watt bulb was attached above the apparatus. The intensity of illumination was adjusted by means of a variac.

Procedure

After 20 trials of retraining on brightness discrimination, training was continued under different levels of ambient room illumination. Ten daily trials were given, and each day illumination was raised over that of the previous day. Table VIII gives the levels of illumination over the 10-day test period. Measurements were made in ft. candles with a Brockwell model S exposure meter whose photocell was either pointing directly toward the cue card from a distance of 4.5 in. or up towards the source of incident illumination.

TABLE VIII

INTENSITIES OF ILLUMINATION DURING BRIGHTNESS DISCRIMINATION

Day	Variac Setting (Volts)	Incident Light	Reflected Light
1	20	< 1 f.-c	3 f.-c
2	25	< 1	3
3	30	< 1	3
4	35	3.5	3.5
5	40	5	3.5
6	45	8	4
7	50	10	4.5
8	55	14	5
9	60	20	6
10	65	28	7

Results

Figure 4 summarizes the results of this experiment. It is apparent that both posterior groups showed an increase in errors at lower levels of incident illumination, unlike the anterior and sham control

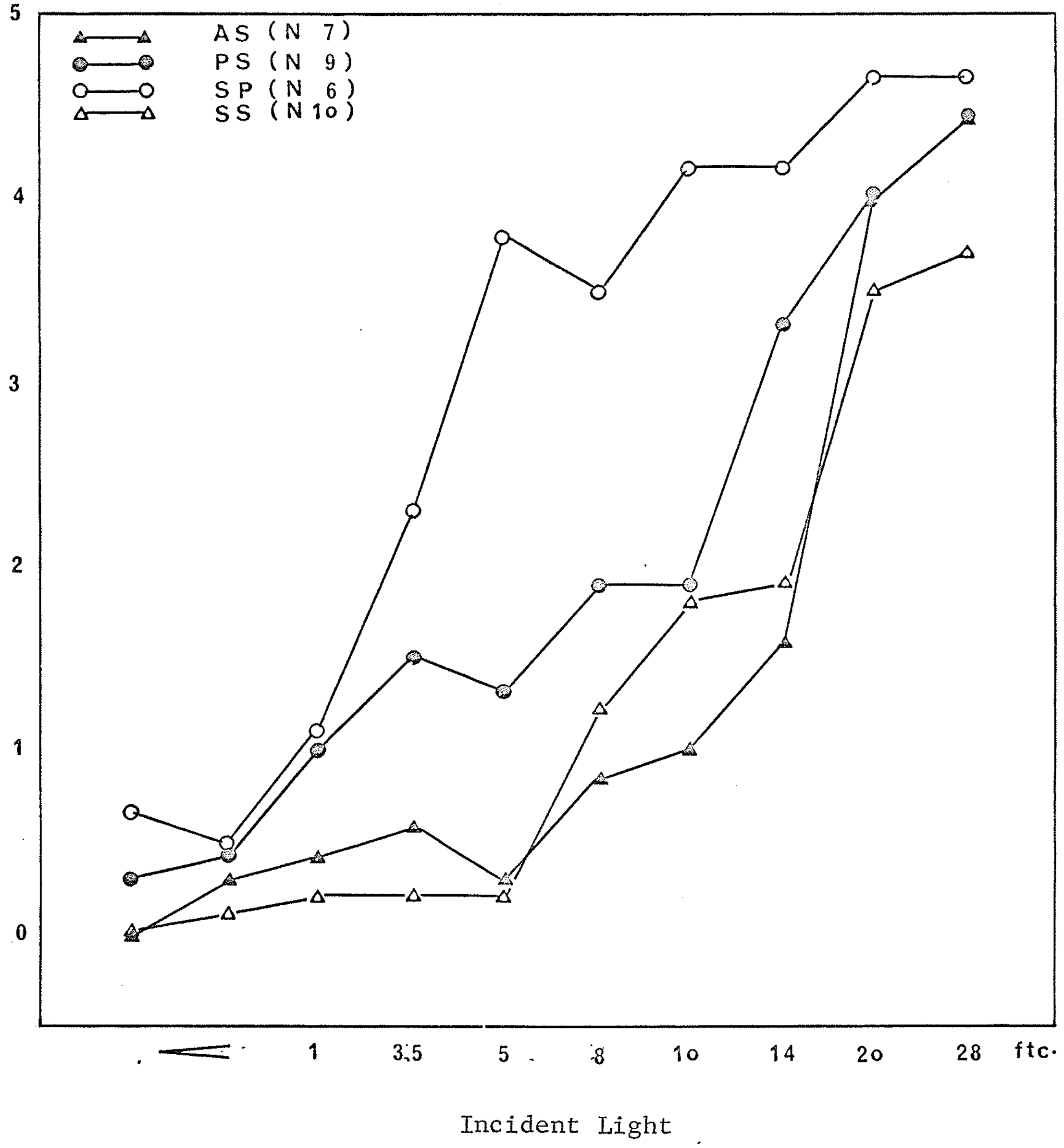

Figure 4. Brightness discrimination under different levels of illumination

groups. All Ss performed nearly perfectly during the first two days of testing. A one-way analysis of variance applied to the transformed total errors for the first 6 days of testing (square-root transformation) yielded an overall F of 112.45 ($P < .001$). The difference between early and late posterior Ss was significant (mean PS errors = 5.88, mean SP errors = 12.00, $t = 2.56$, $p < .02$ /2-tailed/).

Discussion

As expected, striate animals' performance was greatly disturbed by increases in extraneous light stimulation, which confirms previous experiments (Smith, 1937; Bauer & Cooper, 1964). The superior performance of the early lesioned over the later lesioned Ss indicates that some aspects of vision are less affected by early than by late striate removal. However, early lesioned Ss were still deficient in comparison with the controls. As all groups performed at equal levels prior to changes in illumination we are confident that these effects are not due to differences in learning but rather due to differences in visual capacity.

EXPERIMENT VI

RESPONSE TO DEPTH FROM A RAISED PLATFORM

The Problem

It was shown in Experiment I that early posterior cortex lesioned rats can respond normally in a visual cliff test, in contrast to later lesioned Ss, which suggests that some aspects of vision relating to visual depth are less impaired in the former. As a further test of such animals' ability to respond to depth, the present experiment was performed.

Method

Apparatus

The apparatus which is diagrammatically depicted in Fig. 5 consisted of a metal rod and stand. An 8 x 5 in. wooden platform was attached horizontally to the rod by means of a clamp. On either side of the platform were either a 6.5 x 4.5 x 2.75 in. gray cardboard box or a flat piece of cardboard of the same surface area and brightness.

Procedure

E placed a S onto the platform while a second E observed S's behavior and recorded the side to which S would descend. Testing was discontinued if S remained on the platform for 10 minutes. The box and the surface were switched in a R L L R sequence for the total of four trials given. Three different tests were given. In Test I the platform was 4.75 in. above the floor, 2.25 in. from the shallow side, and in Test II, 8.25 in. from the floor and 5.75 in. from the shallow side. For Test III the conditions for Test I were repeated except that Ss had their whiskers removed.

Results

Fig. 6 presents results of tests I and II. It can be seen that, with the platform in the low positions (Task I) the early posterior Ss differed from all others in preferring to step off onto the shallow side. This preference was abolished with the platform in the high position (Task II) where nearly all early posterior Ss failed to descend from the platform. Comparison of the early posterior's responses for tasks I and II, by means of a sign test, yielded a significant difference at $p < .01$ (2-tailed). None of the other Ss differed significantly

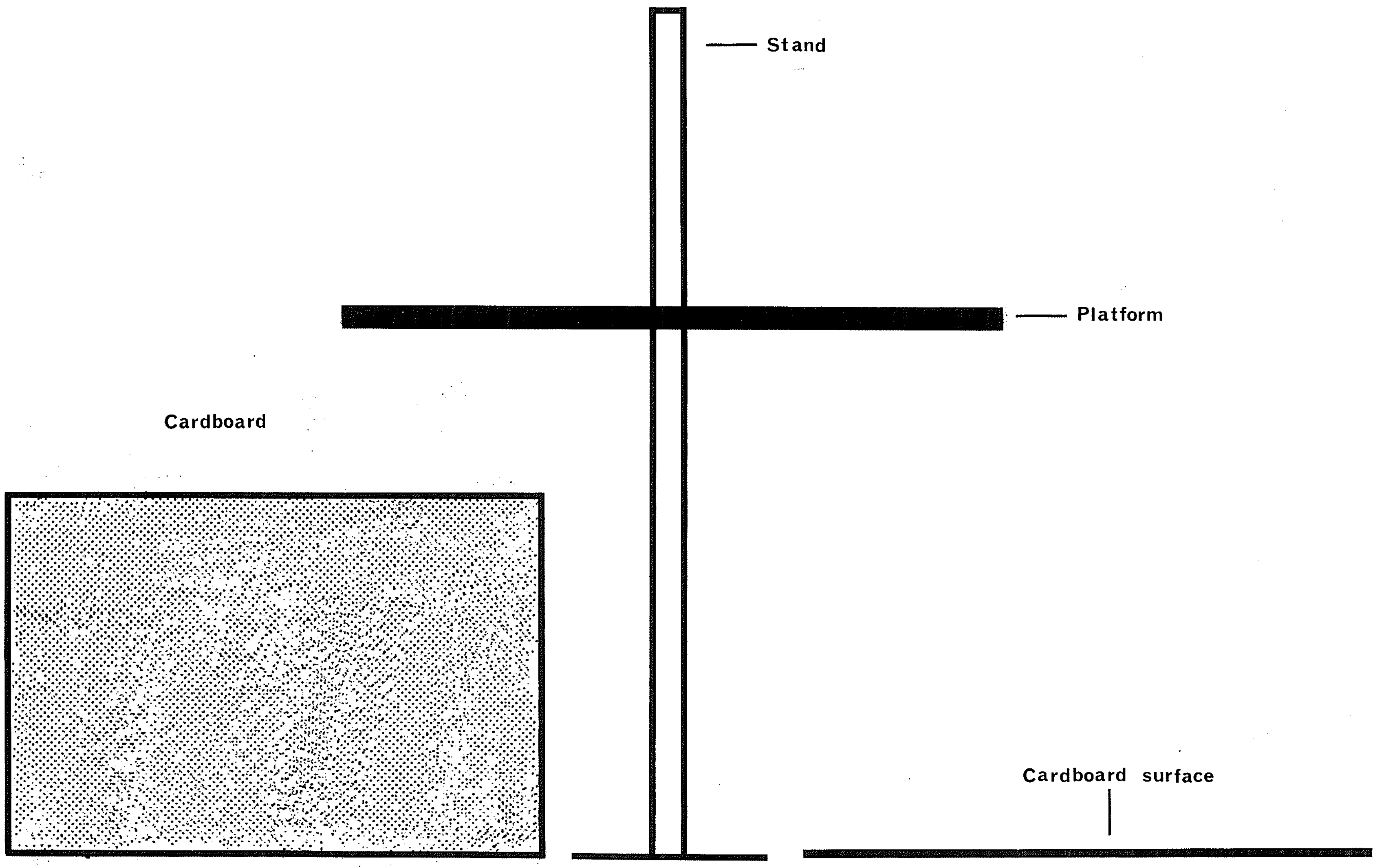

Figure 5. **Apparatus used to test reaction to depth**

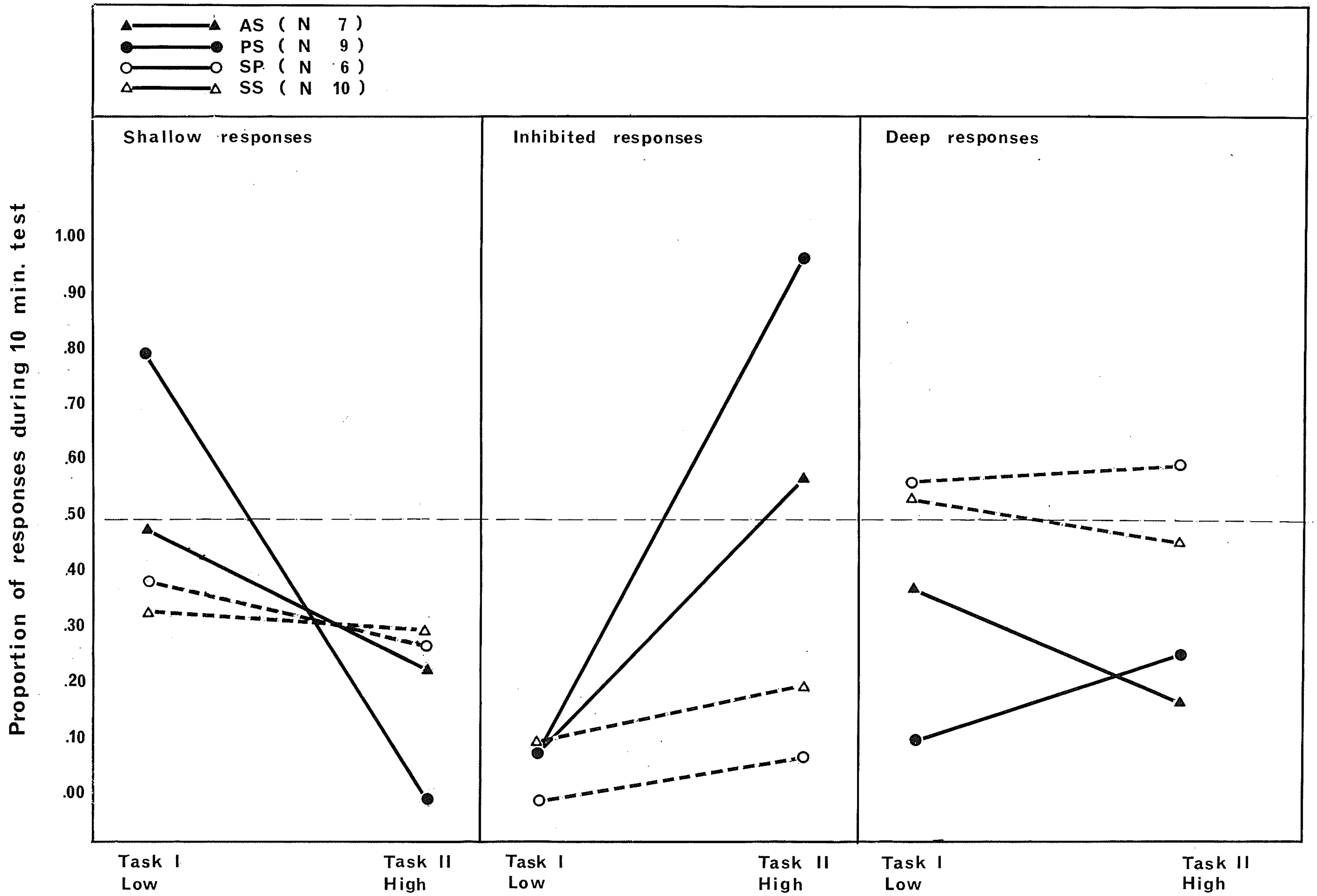

Figure 6. **Response to height from a raised platform**

between Tasks I and II in terms of number of shallow or inhibited responses. The early posteriors differed significantly from the late posteriors on Task I (shallow responses), $U = 8$, $p < .02$ (2-tailed). Comparisons of the groups' performance between Tasks I and III yielded no significant differences.

While in terms of response preference, no differences could be observed between the other groups, differences in response latencies were found (Fig. 7). Inspection shows that late lesioned Ss, (SP), had the shortest response latencies whereas no differences could be seen between the other groups. This finding agrees with the qualitative observations that none of these animals seemed to explore very much when put onto the platform but descended quickly with no preference for any particular direction. Their mode of descent also differed from those of all other rats in that they seemed to 'walk off' the platform, whereas a normal rat would let himself down slowly, often dangling by his hindfeet from the platform.

A one-way analysis of variance was made of the transformed total latencies (Log. transformation) for Tasks I and II which yielded an overall F of 3.88 ($p < .025$). There were no differences in the number of Boli collected for each group at any time.

Discussion

As the foregoing task is analogous to the visual cliff (Experiment I) it is not surprising to find differences in behavior between early and late posteriors. What was surprising was that the early posteriors also differed from the control groups. The best explanation of these data seems to be that these animals have a visual deficit but can see sufficiently well to recognize the 'deep' side and therefore

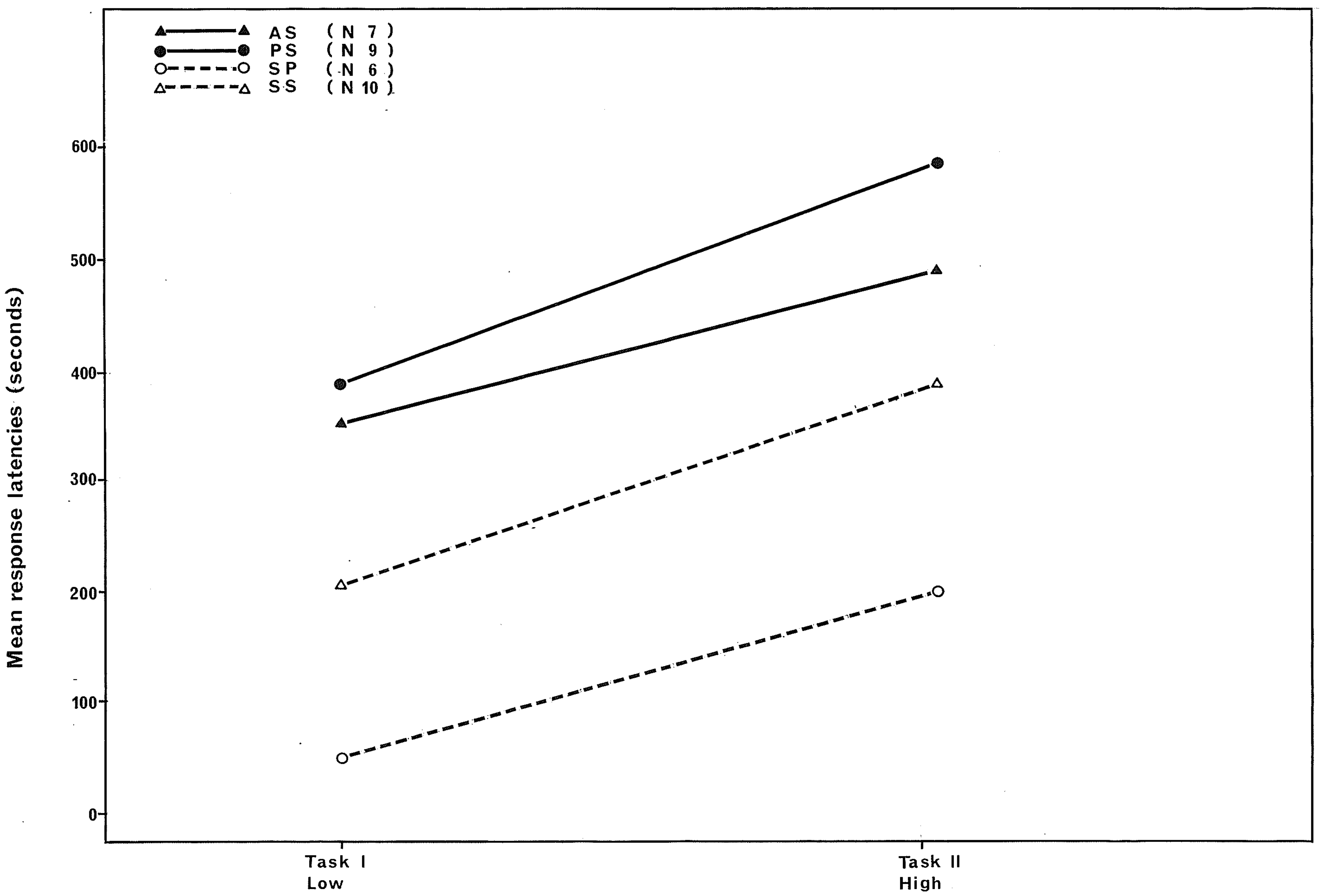

Figure 7. **Response to height from a raised platform**

prefer the shallow side during Task I. During Task II Ss were able to discern the deep side but did not discriminate sufficiently between the deep and the shallow side and therefore inhibited the response. Neither Task I nor Task II represent a real problem for a normal rat, which would explain why none of the control Ss showed any particular preference. The performance of the late posterior Ss represents a problem in that they did not differ in their response preference from the controls. Yet, their lack of exploration and short response latencies suggest that their responses were not made to the visual stimuli of the situation. This is supported by the same Ss' inability to respond in the visual cliff.

These explanations may seem a bit tortuous, but they are not implausible. The main conclusion to be made, however, is that again we were able to demonstrate differences in performance between early and late striate animals in a visual task. That visual factors must have been responsible for the results of the present study is supported by the finding that removal of whiskers did not change the behavior of the animals.

EXPERIMENT VII

BRIGHTNESS DISCRIMINATION REVERSAL

The Problem

Early experiments by Tsang (1934, 1936) have shown that striate removals in enucleated rats will retard maze learning more than enucleation alone. These findings, later confirmed by Lashley (1943), suggest that in addition to its involvement in vision, the striate cortex has a non-sensory function and is presumably important for learning *per se*. That severity of the deficit on maze learning depends on age of lesioning was shown by Landsdell (1953).

The aim of the present study is to determine the extent to which early and late posterior cortex lesions will affect such problem solving as reversal learning. Brush et al. (1961) and Bourke (1954) reported that frontal lesions impair reversal learning. Gonzales, Roberts, and Bitterman (1964) made large combined anterior and posterior lesions and found impairment of reversal learning. Although Krechevsky (1936) reported deficits in brightness discrimination on reversal, no recent data are available on the effects of posterior lesions alone on reversal learning. To provide this information our animals were trained on two brightness discrimination reversals.

Method

Subjects and Apparatus

_S_s of the previous experiments were trained in the Yerkes-type discrimination apparatus depicted in Fig. 2.

Procedure

After 20 trials of retraining on the previously-learned brightness discrimination (white card positive, black card negative) 10 daily trials of reversal training were given (Reversal I) black card positive, white card negative) until a criterion of 18/20 correct trials had been reached. Subsequently, each _S_ began training on the second reversal (Reversal II) which was the same problem as the original discrimination. _S_s were again brought to a criterion of 18/20 correct.

Results

Total errors to criterion for each _S_ and group are shown in Fig. 8, while average errors and trials to criterion are listed in

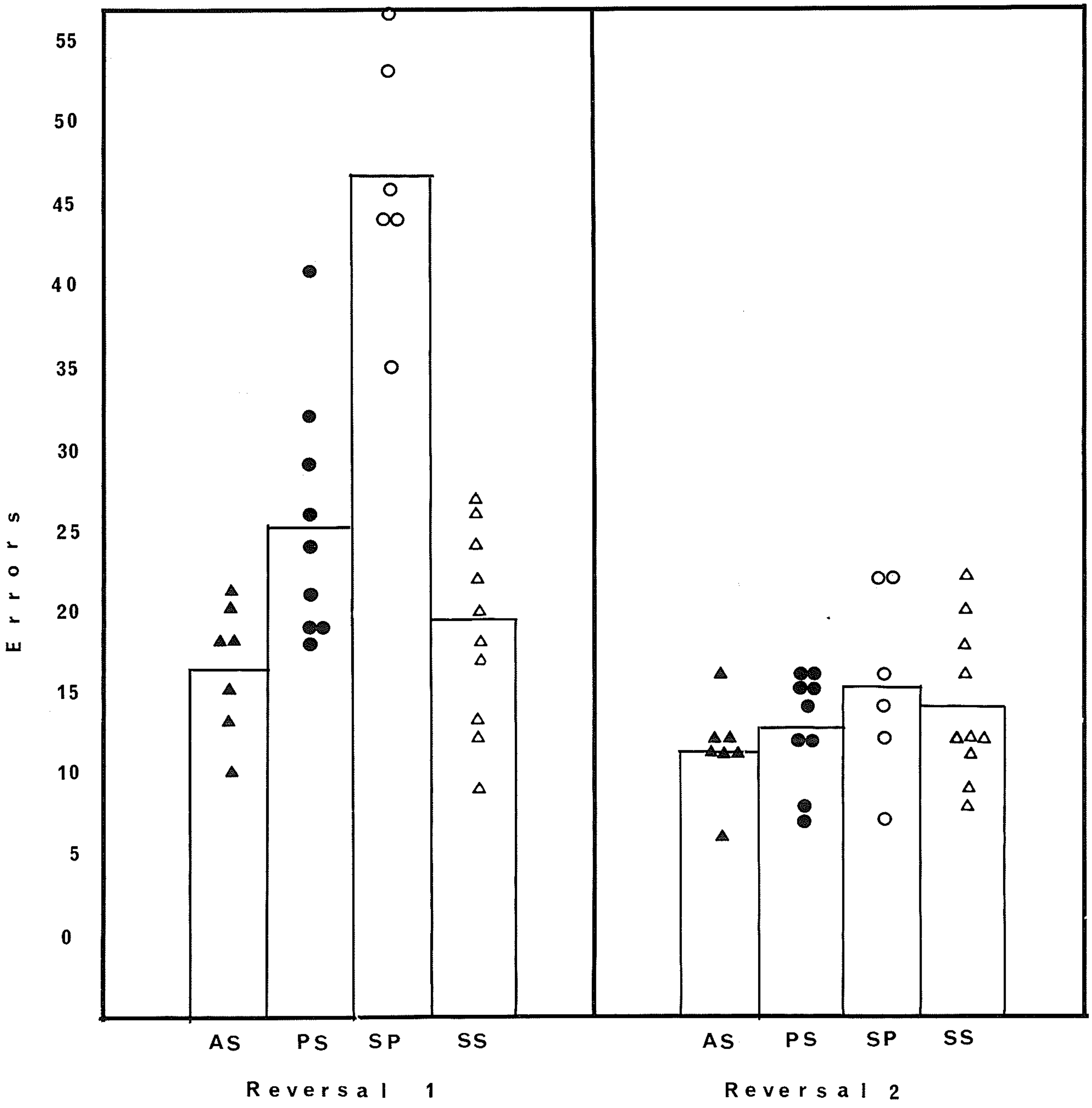

Figure 8. Brightness discrimination reversals

Table IX.

TABLE IX

BRIGHTNESS DISCRIMINATION REVERSALS MEAN ERRORS AND TRIALS TO CRITERION

	AS	PS	SP	SS
REVERSAL I				
Errors	16.42	25.44	47.00	19.70
Trials	40.00	56.11	90.83	46.50
REVERSAL II				
Errors	11.28	12.77	15.50	14.00
Trials	35.71	38.77	49.17	40.50

The error scores were transformed (square-root transformation) and analyzed by means of a one-way analysis of variance. For Reversal I we obtained an F of 19.65 which is significant at $p < .001$. No significant F was obtained for data from Reversal II. Group comparisons for Reversal I yielded significant differences between the PS and SP groups ($t = 4.78$, $p < .001$) and also between the PS and SS groups ($t = 2.15$, $p < .05$). All tests are 2-tailed.

Discussion

It was shown that posterior cortical lesions impair reversal learning, which confirms previous findings of Krechevsky (1936). As similar effects have been demonstrated for frontal animals one suspects that such impairments may be the result of any cortical damage, irrespective of area, and can, therefore, be characterized as being non-specific. All Ss had learned the discrimination to criterion prior to reversal learning, which involved no new cues. We are certain, therefore, that the impairment is not due to sensory deficits. As will be discussed in a later section, our frontal lesions were probably too small and superficial to have an effect on learning. Although early lesioned posteriors were impaired, their performance was significantly superior to that of the later lesioned Ss which demonstrates that early and late posterior lesions will impair problem solving differentially but in a qualitatively similar fashion.

Additional Behavioral Observation

Activity

Two activity tests were given to all Ss; one before the second operation and one after (Activity I and II). Activity was measured in terms of the numbers of squares crossed in a 5-minute period in an open field. The results for the Ss of the various groups can be seen in Fig. 9. Group differences were analyzed by means of a Mann Whitney U test which yielded the results presented in Table X.

TABLE X

RESULTS OF STATISTICAL COMPARISONS
OF GROUPS ON ACTIVITY MEASURES

ACTIVITY I	P vs. S_2,	$U = 17.5$,	$p < .02$
	P vs. S_1,	$U = 9$,	$p < .02$
ACTIVITY II	PS vs. SP,	$U = 20$,	$p > .05$
	PS vs. SS,	$U = 10.5$,	$p < .02$
	SP vs. SS,	$U = 2$,	$p < .002$
	AS vs. SS,	$U = 4$,	$p < .02$

All p values are 2-tailed

While increases in activity as a result of anterior cortical removals are well-established (Beach, 1941; Zubek & De Lorenzo, 1952;

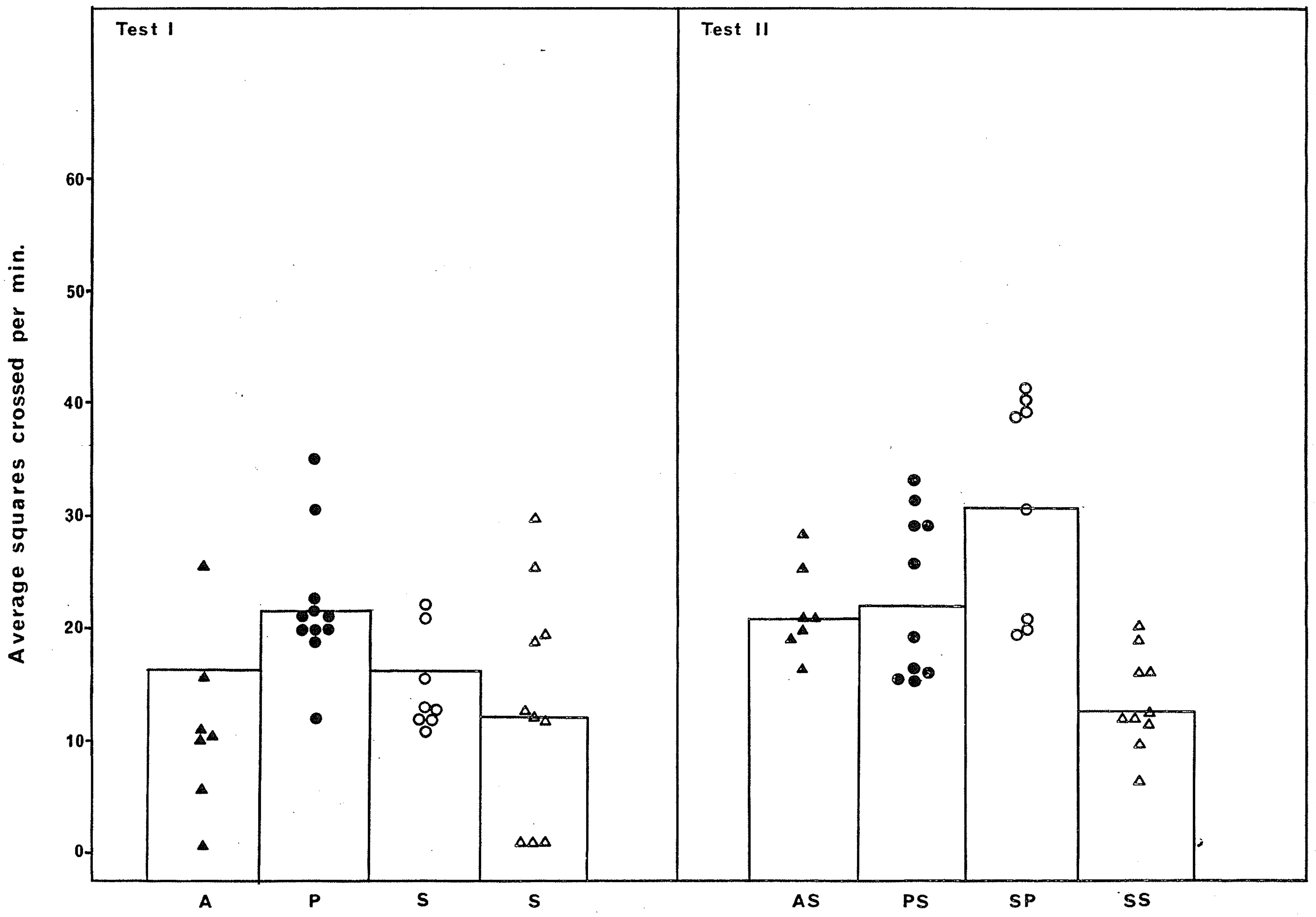

Figure 9. **Activity in open field**

Morgan, 1965), the effect of posterior lesions are equivocal. Some investigators reported increases in activity (Beach, 1941; Altman, 1962) while others failed to observe increases. The basic problem is that most studies differ from each other in methodology. The present study is the first which showed increased activity as a result of posterior lesions and as measured by open field behavior. Further, it is interesting to note that the effects were independent of the age at which the lesion was made.

Shock-Avoidance Behavior

It will be recalled that in all tasks using the Yerkes-type discrimination apparatus (Fig. 2) shock motivation was used (see Experiment III). In addition to being punished for errors by foot shock through either grid I or II, Ss received shock at regular intervals until they had left the start and discrimination chambers. As casual observations from previous studies suggested that posterior Ss might be deficient in avoidance behavior we decided to record, by means of an electric counter, all the footshocks given while the Ss were on Grid III. The total number of shocks per animal for a given task was divided by the number of trials taken to reach criterion, (except for Experiment V) and plotted in bargraph form.

Figures 10, 11, 12, and 13 show the number of shocks taken by each animal in the various experiments using the discrimination situation and shock motivation. It is apparent that in all instances, the posterior groups took a greater number of shocks than the controls; except for the initial avoidance learning (Fig. 10), where all operated Ss took more shocks than the shams. Furthermore, these effects were independent of the time at which the surgery was performed, as there were no

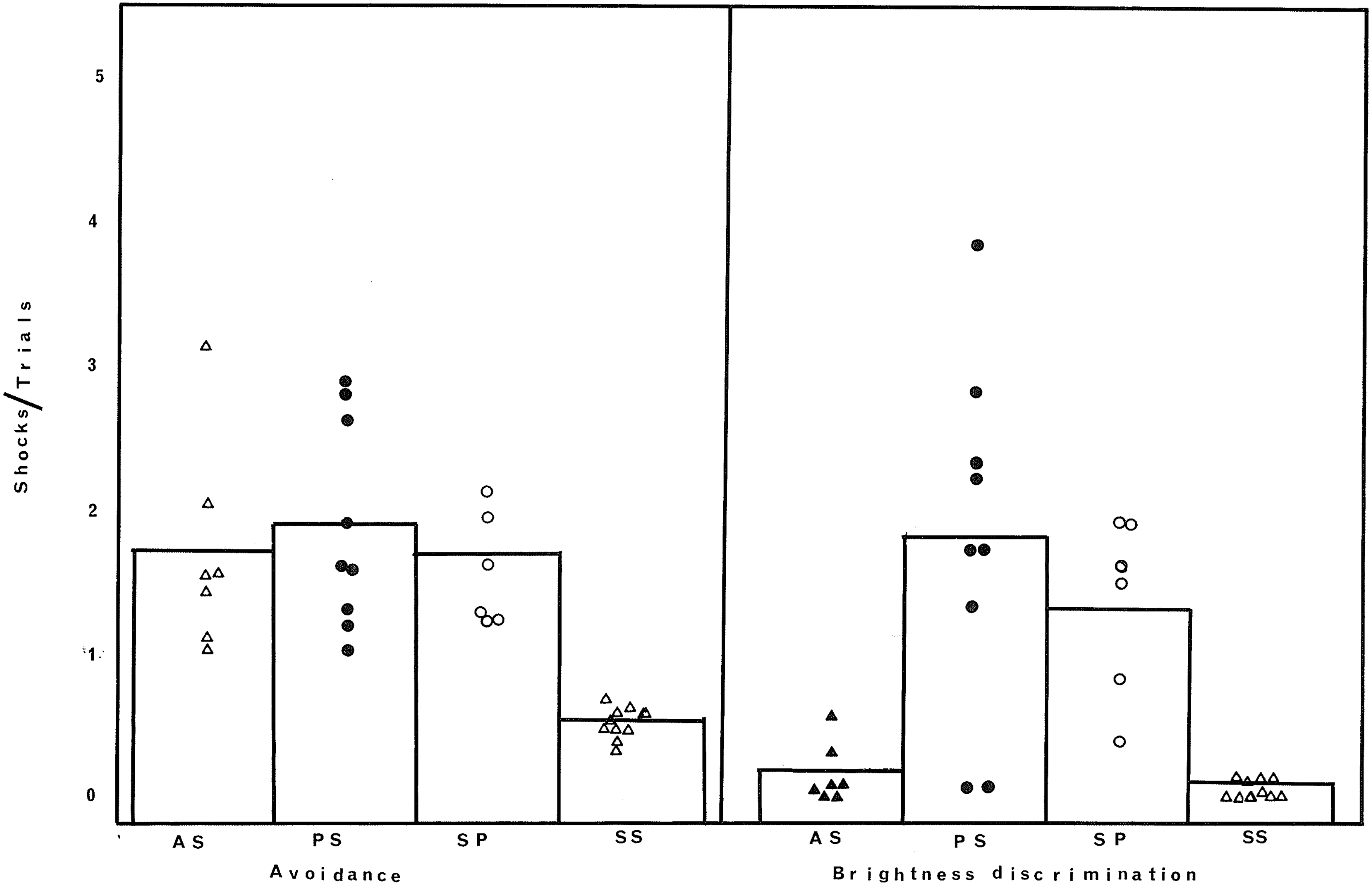

Figure 10. Number of shocks given during training

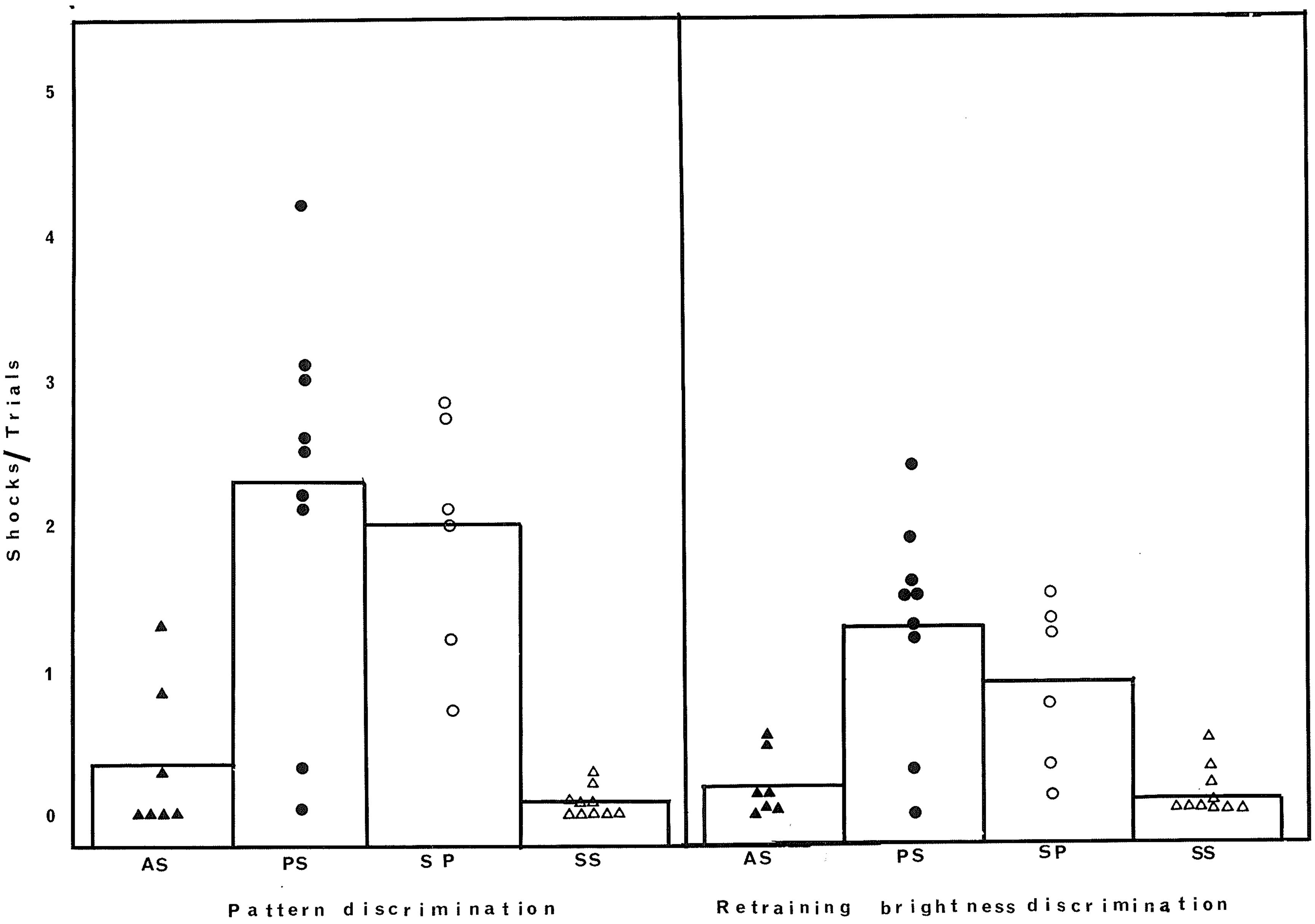

Figure 11. Number of shocks given during training

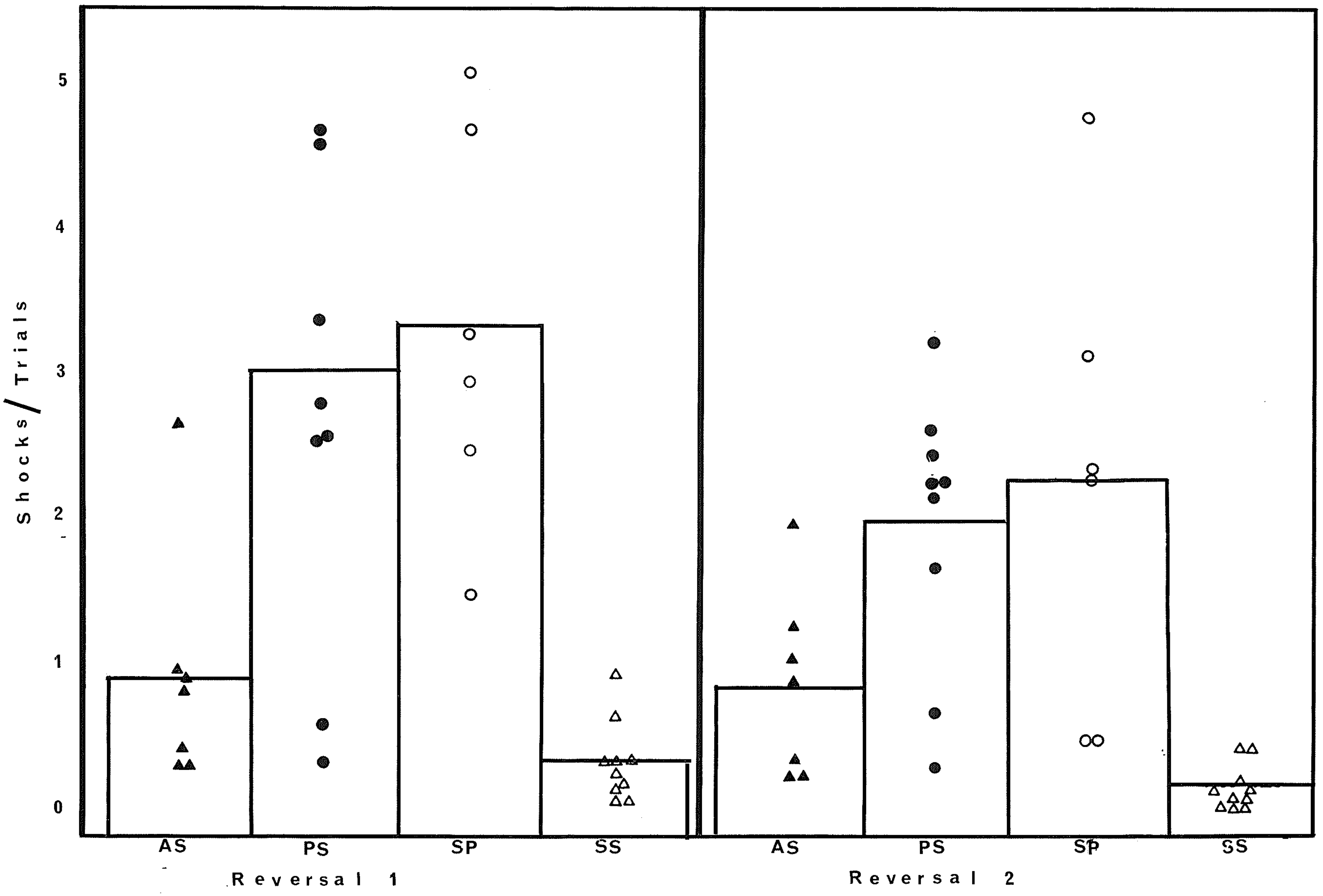

Figure 12. Number of shocks given during brightness discrimination reversal

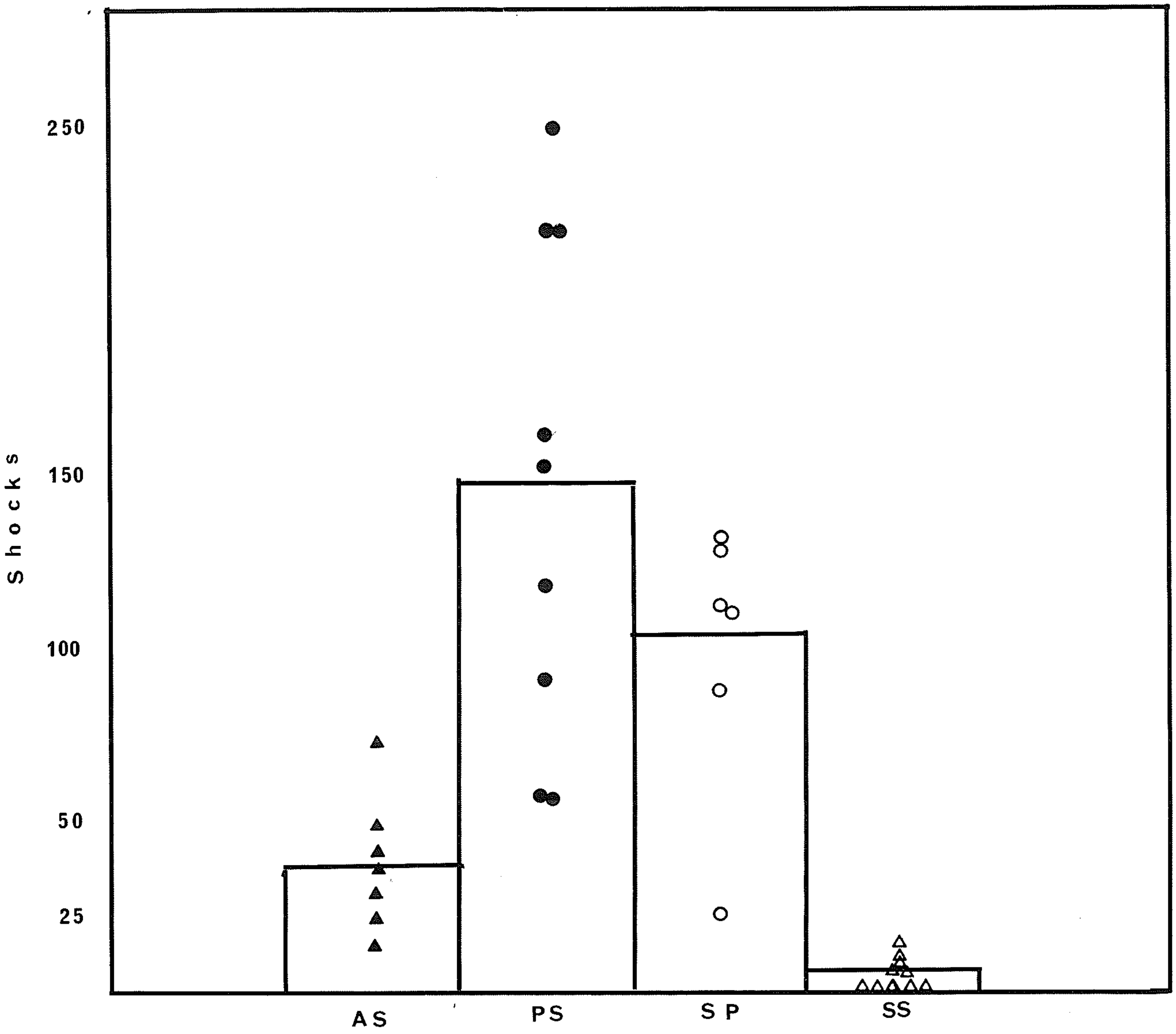

Figure 13. Number of shocks given during brightness discrimination training under varying levels of illumination

differences between early and late posterior lesioned Ss. Statistical analysis was made of the doubtful cases only (Fig. 10, brightness discrimination, Fig. 11, pattern discrimination) and in no instance were the differences between PS and SP groups significant.

Although it is not possible to rule out visual deficits as having been responsible for impaired avoidance, it seems unlikely for several reasons. First, Ss would reach criterion on learning the various tasks without noticeable improvement in avoidance. Secondly, on comparing data for brightness discrimination (Fig. 10) and those for retraining of the same discrimination (Fig. 11) one finds little difference in the shock data, although nearly all Ss showed perfect retention of the discrimination during retraining.

Krechevsky (1936) noted that differences in rates of brightness discrimination learning between striate and normal rats can be reduced by the use of shock for punishment, which he interpreted as being due to differences in 'levels of attention' between the groups. Our finding that shock avoidance behavior is impaired suggests, however, that such animals differ in terms of motivation. That visual cortex lesions impair shock avoidance behavior, has recently been confirmed by Lubar (1967), who observed impaired shock avoidance learning in the cat. Similarly, Pinel (1967)[4] has found that even extremely small striate lesions impair avoidance in the rat. Lubar's lesions were too small to interfere with pattern discrimination learning, which agrees with our suggestion that impairment of shock avoidance is not due to visual deficits. The possibility cannot be ruled out, however, that impaired avoidance may be in part responsible for observed deficits in learning certain visual tasks, when shock motivation is employed.

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[4] Personal communication, May, 1967.

Anatomical Results

Survival rates, body and organ weights, eye examinations

Deaths at the time of neonatal lesioning and weaning were minimal, as is apparent from the following survivals: Anteriors 81%, Posteriors 78%, Shams 93%. These figures contrast with those of Schwartz (1964) who reported a mortality rate of 50% for his neonatally lesioned Ss.

Body weights were taken at 21, 38, 52, 63, and 210 days of age, and at no time were there any significant differences between any of the groups. Before Ss were killed their eyes were examined. All showed normal light reflexes and most of them had normal eyes. A few Ss in each group appeared to show some pallor of the optic disc in one or both eyes. However, the examining ophthalmologist questioned his observations as they could have been due to variability in the examining technique.

Finally, Ss were killed with ether, their brains perfused with saline and formaline, and weight determinations made of the following: testes, adrenals, pituitary, pineal, seminal vesicles and prostate glands. None of these differed significantly for the various groups.

Histological Results

After removal from the skull the brains were hardened in formalin, and cut into 30 u thick slices by means of a freezing microtome. Every sixth section was saved and mounted on slides. Subsequently, sections were stained with the cell and fibre stain described by Klüver and Barrera (1953). Using a Bausch and Lomb microprojector, every third section was drawn and the lesions were reconstructed on Lasley-type diagrams. These diagrams are presented in Appendix A and give an indication of the dorsal extent of the damage. Indications of the depth of the lesion are given by two diagrams of horizontal sections for each brain. Question marks indicate that parts of the brain were lost in making the slides. Lesions of the anterior control groups were very small in extent and superficial in depth. and only a dorsal view of the lesions is presented.

Inspection of the posterior lesions revealed that in all but possibly 2 SS (PS 11-5, 8-1) areas 17, the primary visual projection areas as designated by Krieg (1946), had been completely extirpated. The data of these Ss were, however, analyzed together with the data of the other Ss, as all Ss were unable to learn the pattern discrimination, which is usually considered an indication of complete removal of the striate areas. Although degeneration of cells in the lateral geniculate bodies is considered proof of removal of the visual areas, we believe that in view of the size of the lesions and also the behavioral data, mapping of geniculate degeneration was neither crucial nor necessary.

Descriptions of Lesions

A. Early and late posteriors. Most posterior lesions were fairly uniform. In addition to area 17, areas 7, 18, and 18a were destroyed in most cases. Anteriorly, somesthetic cortex was invaded and the auditory cortex was damaged laterally, some lesions extending as far as the rhinal fissure. In addition to cortical tissue, fibres of the underlying corpus callosum were always destroyed, and in some Ss, usually unilateral, invasion of subcortical structures such as the hippocampus could be seen. All brains were examined for subcortical damage and the results are summarized in Table XI.

TABLE XI

SUBCORTICAL DAMAGE IN POSTERIOR LESIONED ANIMALS

	TYPE OF LESIONS					
STRUCTURE	SMALL		MEDIUM		LARGE	
	unilat.	bilat.	unilat.	bilat.	unilat.	bilat.
Head of	PS# 11-4	SP# 9-7	-	-	-	-
caudate n.	SP# 10-1	-	-	-	-	-
Alveus	PS# 11-5	PS# 11-4	-	-	-	-
	PS# 8-1	PS# 11-3	-	-	-	-
	PS# 3-3	PS# 3-2	-	-	-	-
	PS# 3-4	SP# 9-2	-	-	-	-
	PS# 3-8	SP# 9-7	-	-	-	-
	SP# 10-1	-	-	-	-	-
	SP# 6-7	-	-	-	-	-
Hippocampus	-	-	SP# 4-5	-	-	-
	-	-	PS# 11-4	SP# 9-7	SP# 6-5	-
	-	-	SP# 10-1	-	-	-
	-	-	SP# 6-7	-	-	-

The type of involvement was characterized in terms of size and depth of damage. For example, a 'small' lesion is one which could be seen in a few sections only and was superficial in depth. For the hippocampus this means involvement of the alveus only, without damage to the pyramidal layer. A large lesion was one which extended throughout the structure, in an anterior posterior extent, and in the case of the hippocampus would involve the pyramidal and deeper layers. As can be seen from Table XI, there were no systematic differences between the two groups with regard to subcortical involvement. In addition, most subcortical involvement was unilateral and very slight. Damage to the hippocampus was not related to performance in the various experiments.

B. Anteriors. From inspection of the diagrams (Appendix A) it is apparent that the anterior Ss could not serve as a control for amount of cortical tissue removed, but only as a control for cortical damage per se. Without exception these lesions were found to be extremely variable in size and locus and on the whole were smaller than the posteriors. The reason for this is that we found the frontal cortex in neonate rats not very accessible, particularly as we wished to avoid damage to posterior cortex in these animals.

CHAPTER III

STUDY II

The Problem

Study I demonstrated that striate rats, operated at birth, were superior to Ss operated as adults in performing some visual tasks, while showing equal impairments in other visual and non-visual behaviors. Visual cliff data indicated that some aspects of pattern vision must remain intact in neonatally lesioned Ss, while performance of a classical pattern discrimination suggested that pattern vision as required by that particular task was abolished. Apart from differences in the stimulus conditions, there were differences in the motivating conditions. Finally, all Ss exhibited deficient shock avoidance behavior, and the question arose whether the pattern discrimination deficit could have been due to a complex interaction of sensory, perceptual, and motivational factors. However, before the importance of these various factors to the pattern discrimination deficit can be studied indpendently, it is necessary to obtain more information about the effects of posterior cortex lesions on shock-motivated behavior.

The aim of the present study was two-fold: first, we wished to discover whether the use of drugs, known to have specific effects on avoidance behavior, can possibly change the differences between normal and striate rats in learning a visual task using shock motivation. Secondly, we wanted to study directly posterior animals' reactions to various levels of shock, as well as their ability to learn a passive avoidance task. We hoped that the results of this study would not only facilitate interpretation of existing data, but also lead to further meaningful questions concerning the effects of posterior neocortical lesions on behavior.

EXPERIMENT VIII

BRIGHTNESS DISCRIMINATION UNDER AMPHETAMINE

The Problem

The question was asked, whether the inability of striate rats to learn a pattern discrimination in a Yerkes-type task, using shock motivation, could have been due to changes in motivation. Some studies have shown that administration of amphetamine improves shock-avoidance performance (Hearst et al., 1963; Krieckhaus et al., 1965a, b). In addition, amphetamine has been found to counteract the effects of lesions which disrupt avoidance learning (Krieckhaus, 1965b).

The present study was made to investigate the possibility that shock avoidance behavior of striate rats can be improved by the use of amphetamine. If brightness discrimination performance also improved, further experiments using amphetamine during pattern discrimination learning would be in order. On the other hand, should visual deficits persist despite the improvement in shock avoidance performance, we could be more confident in excluding motivation as a factor in the impaired performance in visual tasks.

Method

Subjects

Thirty-four, 55 day-old male hooded rats were obtained from the Quebec Breeding Farms. Half of the Ss received posterior neocortical ablations, according to the procedure outlined in Study I, while the other half were sham operated. After a two-week recovery, the surviving

Ss were randomly assigned to the following groups: Posterior/Amphetamine, (n = 7), Posterior/Saline (n = 8), Sham/Amphetamine (n = 8), Sham/Saline (n = 8).

Procedure

Following recovery, training on a brightness discrimination task in a Yerkes-type discrimination box (Fig. 2) was begun, according to the procedure described for Experiment III. In addition, 15 min. prior to the 10 daily trials, amphetamine or saline injections were given (dl- amphetamine, 1 mg/kg, i.p.). Training and injections were discontinued as soon as a S had reached the required criterion of 18/20 correct trials.

Results

It can be seen from Table XII that both posterior groups needed a greater number of trials and made more errors to reach criterion than the shams.

TABLE XII

BRIGHTNESS DISCRIMINATION UNDER AMPHETAMINE

		P (amp.)	P (sal.)	S (amp.)	S (sal.)
	N	7	8	8	9
ERRORS					
Total		72	76	33	30
Mean		10.02	9.50	4.12	3.33
TRIALS					
Total		300	330	200	250
Mean		42.85	41.42	25.00	27.77

The transformed error scores (square-root transformation) were analyzed by means of a one-way analysis of variance, which yielded a significant F of 9.81 ($p < .001$). It can be seen from Fig. 14, that apart from the difference in distribution, there were no differences in the number of errors between the amphetamine and saline treated groups.

Figure 15 depicts the number of shocks taken by the various groups during learning. The means and the results of the statistical tests are presented in Table XIII.

TABLE XIII

AVERAGE SHOCKS GIVEN DURING BRIGHTNESS DISCRIMINATION UNDER AMPHETAMINE AND RESULTS OF STATISTICAL TESTS

	P (amp.)	P (sal.)	S (amp.)	S (sal.)
N	7	8	8	9
Mean	1.040	1.252	.137	.122

P (amp.) = P (sal.) $U = 28$, $p > .05$ (2-tailed)
" ≠ S (amp.) $U = 5$, $p < .01$ "
" ≠ S (sal.) $U = 7$, $p < .05$ "
P (sal.) ≠ S (amp.) $U = 5$, $p < .002$ "
" ≠ S (sal.) $U = 3$, $p < .005$ "
S (amp.) = S (sal.) $U = 33$, $p > .05$ "

Mann Whitney U test.

There were no differences between amphetamine and saline treated groups, and all posterior _Ss_ took significantly more shocks than the shams.

Discussion

These results do not differ from those found in our previous study, in terms of either errors or number of foot shocks. In view of existing studies showing improvement in avoidance behavior after amphetamine treatment, it is surprising that our amphetamine treated

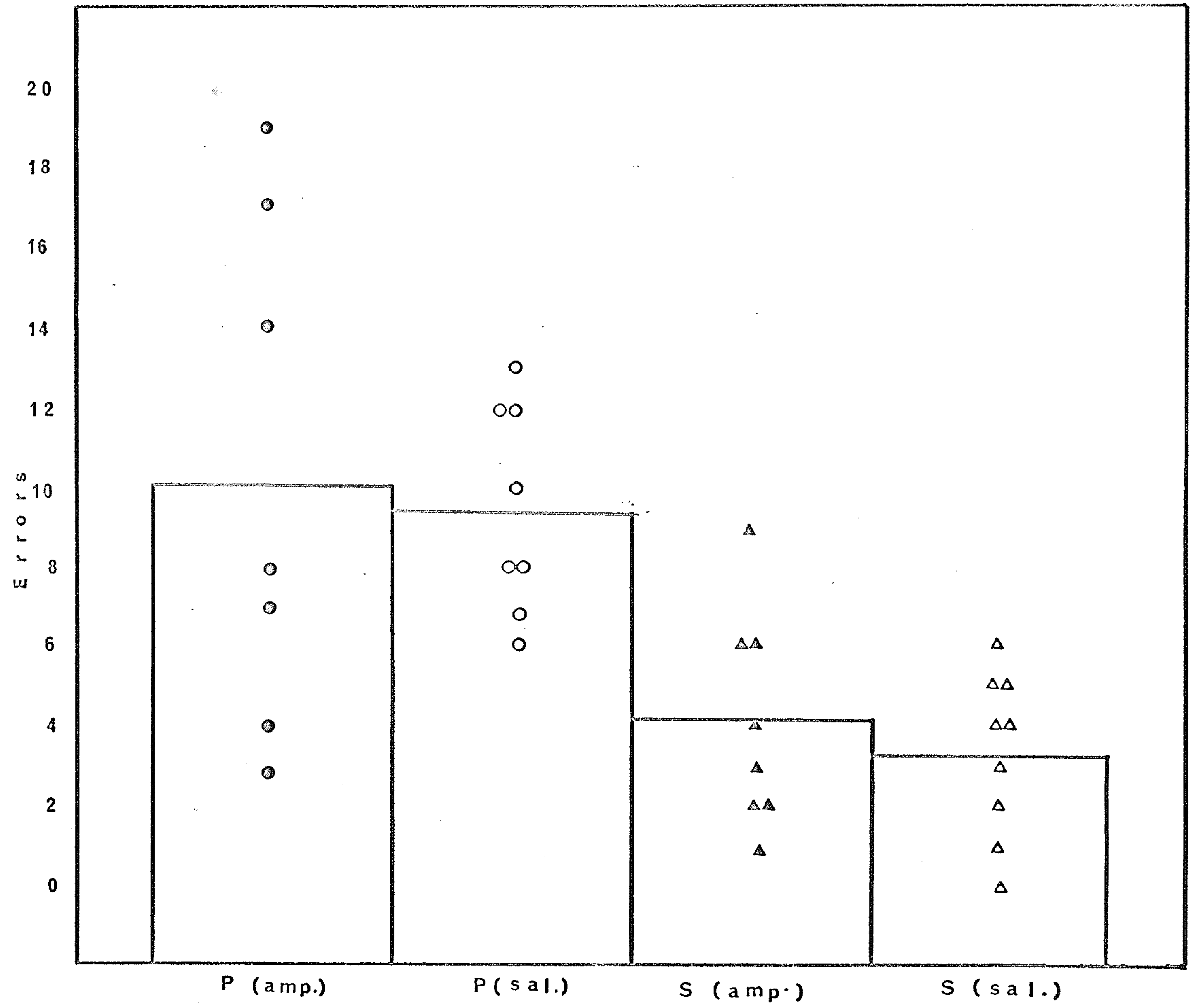

Figure 14. Brightness discrimination under amphetamine

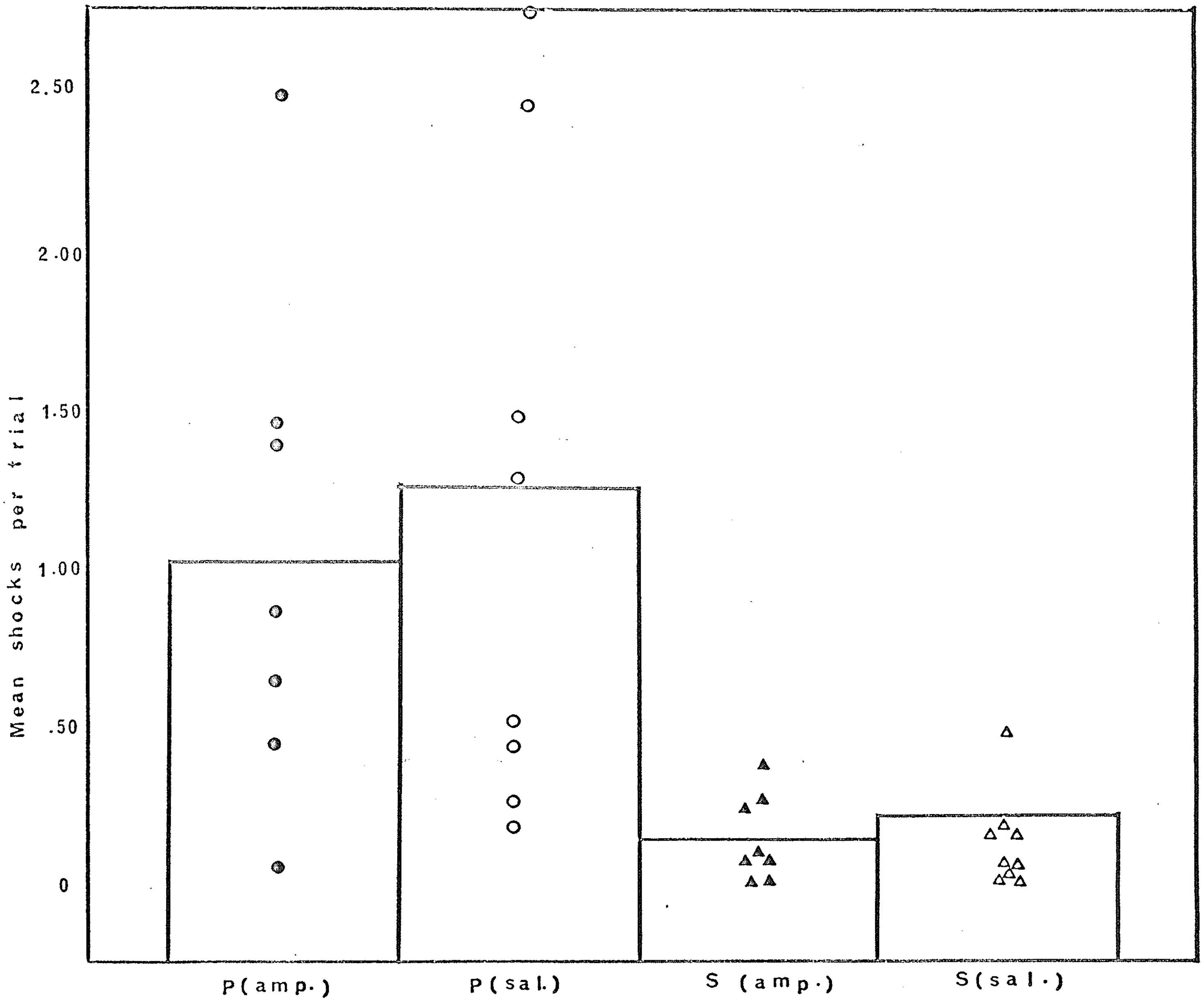

Figure 15. Shocks given during brightness discrimination under amphetamine

groups did not show better performance. The important variable here is the dosage used. Krieckhaus (1965a, b) gave 2 mg/kg whereas we used 1 mg/kg only. Our choice of dosage, however, was determined by the observations of Braun et al. (1966), which suggest that higher dosages might result in visible sympathomimetic responses, and so interfere with behavior. In addition, the same investigators showed that even with a 1 mg/kg dose, postoperative performance of a brightness discrimination would improve. However, we are forced to conclude that the dosage used in our experiment may not have been sufficiently large to produce the desired effects.

EXPERIMENT IX

RESPONSE TO SHOCK AT VARIOUS CURRENT INTENSITIES

The Problem

As earlier demonstrated, striate rats are deficient in shock avoidance learning, a finding which was confirmed by recent studies on the cat (Lubar, 1967). It is not known, however, whether striate lesions act by changing the sensitivity to painful stimulation or in some other unknown fashion. Both hypo- and hypersensitivity to shock could be responsible for this impairment. It is, therefore, of interest to determine whether striate and normal subjects react differently at various shock levels, in terms of their natural reactions to such stimulation as startle, tailflick, and vocalization.

Method

Subjects

Ss were the same as used for the previous experiment. As there were no differences between amphetamine and saline treated groups, they were pooled to obtain two groups of posteriors and shams of 17 Ss in each.

Apparatus

The first apparatus consisted of a 32 x 32 x 9.5 in. open field with the floor made of 1/8 in. metal rods, placed 1/2 in. apart, through which foot shock could be administered by means of a variable current source.

The second apparatus was a clear plastic restraining tube, with airholes and an opening for the tail of the animal.

Procedure

A. Open field testing. Each S was placed in the center of the field and allowed to explore for 5 minutes. Thereafter 1/2 second foot shocks were given, but not more than one each of the following intensities: .100, .125, .160, .250, .500, .750, 1.000, 1.250, 1.500, 1.750, and 2.000 ma. These were given in an ascending series, from the weakest to the strongest, and within variable intervals, ranging from 5 to 20 seconds. Only in case of a doubtful response was a stimulus repeated. E noted intensities at which (1) startle and (2) vocalization first occurred.

B. Restraining tube testing. The day after the open field testing, each S was put into the plastic tube and restrained by inserting the bottom piece, which allowed unrestrained movement of the tail only. The tube was then placed horizontally on a table with the S's tail hanging down over the edge. To assure good contact with the electrode the tail was cleaned with a piece of cotton soaked in saline, and then dried with Celluwipes. The 'neutral' wire was wound around and taped to the base of the tail, while the 'hot' wire was similarly fastened to the middle. Current bursts of 1/2 second duration were given in the same fashion as described earlier. E noted intensities when tailflick and vocalization first occurred, after which testing was discontinued.

Results

Table XIV presents the number of Ss responding at various levels of current intensities, while the average response intensities and results of a Mann Whitney U test are presented in Table XV. All p values reported are 2-tailed. It was found that the shams startled and vocalized at significantly lower intensities of shock than the posteriors in the open field test. Furthermore, vocalization usually occurred at higher intensities and never occurred before startle. Differences in intensities at which vocalization first occurred were also seen in the restraining tube test and again the shams vocalized at significantly lower intensities of shock than the posteriors. By contrast, no significant differences between the groups were observed for the tailflick response.

TABLE XIV

REACTIONS AT VARIOUS LEVELS OF ELECTRIC SHOCK CURRENT INTENSITIES AT WHICH SUBJECTS FIRST RESPONDED

Open Field

	Startle		Vocalization	
ma.	posteriors	shams	posteriors	shams
.100	1	3	-	1
.125	2	6	-	-
.160	1	7	1	7
.250	11	-	1	6
.500	2	1	10	3
.750	-	-	4	-
1.000	-	-	1	-
1.250	-	-	-	-
1.500	-	-	-	-

Plastic Restraining Tubes

	Tailflick		Vocalization	
ma.	posteriors	shams	posteriors	shams
.100	5	10	-	3
.125	11	7	1	7
.160	-	-	3	3
.250	1	-	9	4
.500	-	-	4	-
.750	-	-	-	-
1.000	-	-	-	-
1.250	-	-	-	-
1.500	-	-	-	-

TABLE XV

REACTIONS AT VARIOUS LEVELS OF ELECTRIC SHOCK AVERAGE INTENSITIES AT WHICH RESPONSES FIRST OCCURRED AND RESULT OF STATISTICAL TESTS

	Open Field		Restraining Tube	
STARTLE				
Posteriors	.250	$U = 54$,	-	
Shams	.157	$p < .02$	-	
TAILFLICK				
Posteriors	-		.125	$U = 98.5$
Shams	-		.110	$p > .10$
VOCALIZATION				
Posteriors	.553	$U = 34$	.285	$U = 45$
	.248	$p < .002$	.156	$p < .002$

Discussion

The open field data seem to indicate that striate lesions decrease a S's sensitivity to painful shock, as inferred from the higher intensities of shock needed to produce startle and vocalization in such animals. Such interpretation fails to hold up, however, for the tailflick data in the restraining tube test. No differences in intensities at which tailflick occurred could be observed, although again there were differences in vocalization. One explanation of such findings would be that tailflick is a more primitive, reflexive response to a painful stimulus whereas vocalization is more complex, involving the perception of the nature of the stimulus. Anthropomorphically, the striate rat may 'feel' a painful stimulus the same way a normal animal does, however, the meaning of the stimulus, as well as the response may be different. Without wanting to push the comparison too far, it is of interest that changes in reactivity to painful stimulation, as a result of cerebral lesions, have been reported for humans (Sweet, 1959). At a more general level, the present study supports the conclusion that in addition to visual and non-sensory functions, the visual cortex may be involved in the perception of and in reaction to noxious stimulation.

EXPERIMENT X

PASSIVE AVOIDANCE

The Problem

It was demonstrated that striate rats are deficient in active avoidance learning, and also, that this effect could be due to a changed reactivity to shock as a result of the lesion. The present experiment was performed to determine whether this changed reactivity is sufficiently general to affect performance of other avoidance tasks, such as passive avoidance, in a similar disruptive manner.

Method

Subjects

The *S*s used were those from the previous experiment.

Apparatus

A wooden box (60 x 7 x 7.5 in.) served as a straight runway. A metal spout, from the waterbottle attached to the outside of the box, projected through a drill hole into the goalbox of the runway. The floor in front of the spout was an 8 x 6 in. aluminum plate. Wires from the shock source were attached to the plate as well as to the spout. With the current turned on a *S* would receive shock as soon as it touched the spout.

Procedure

All Ss were put on a water deprivation schedule during which they were watered for only 15 minutes daily in their home cages. After three days of deprivation Ss were placed two at a time in the start section of the runway and allowed to explore. If they found the water at the end they were permitted to drink for 15 minutes. The following day 10 minutes exploration was given, and the day after Ss were put singly into the runway for 10 minutes. During the preceding, as well as during subsequent training, all Ss were watered upon return to their home cages. Care was taken to water Ss at about the same time each day.

For training Ss were placed in the start section and allowed to run into the goal section. After a couple of licks from the spout Ss were removed and again placed in the start section for a new trial. Ten daily trials were given until Ss ran at a fairly even speed. On subsequent days the spout was electrified on the fifth trial, only after which another five trials were given. On each day the current was increased as follows: (1) .100, (2) .160, (3) .250, (4) .500, and (5) .750 ma. Latencies were measured for the time it took Ss to run from start to goal section. If Ss had not reached the goal section within 30 seconds they were picked up and placed into the goal section and allowed 10 seconds, in which they could drink, before they were returned to the start section for a new trial. E also recorded the number of trials in which no drinking was seen.

Results

It can be seen from Figure 16 that from the third day onward (at .250 ma.) shams showed a greater increase in latencies than the posteriors. These differences between the groups were significant for the .250 and .500 ma. shock levels (.250 ma: $U = 55$, $p < .02$; .500 ma: $U = 61.5$, $p < .05$, /2-tailed/). The differences were not significant at the .750 ma. level ($U = 86$, $p > .10$ /2-tailed/). The number of trials during which drinking was completely inhibited are presented, for each animal, in Fig. 17. It is apparent that fewer posteriors inhibited to the extent that the shams did ($U = 54.5$ $p < .02$, /2-tailed/).

Discussion

These data support the conclusion that striate removal not only changes reactivity to shock and active avoidance performance, but also interferes with passive avoidance. This is confirmed by the finding that latencies of normal *S*s increased earlier and at lower levels of shock intensity than those of striate rats. Further support is derived from the observation that posterior *S*s inhibited drinking on fewer trials than the shams. There is no evidence available which suggests that striate *S*s have higher thirst motivation, nor were there any differences in body weight between the groups after they had been watered every day for the same time. Although such changes in thirst motivation cannot be ruled out until further study, we believe that the present data are in agreement with what one might expect from the preceding experiment. It must be concluded that, independently of the type of avoidance task used, active or passive, striate lesions interfere with avoidance behavior in general.

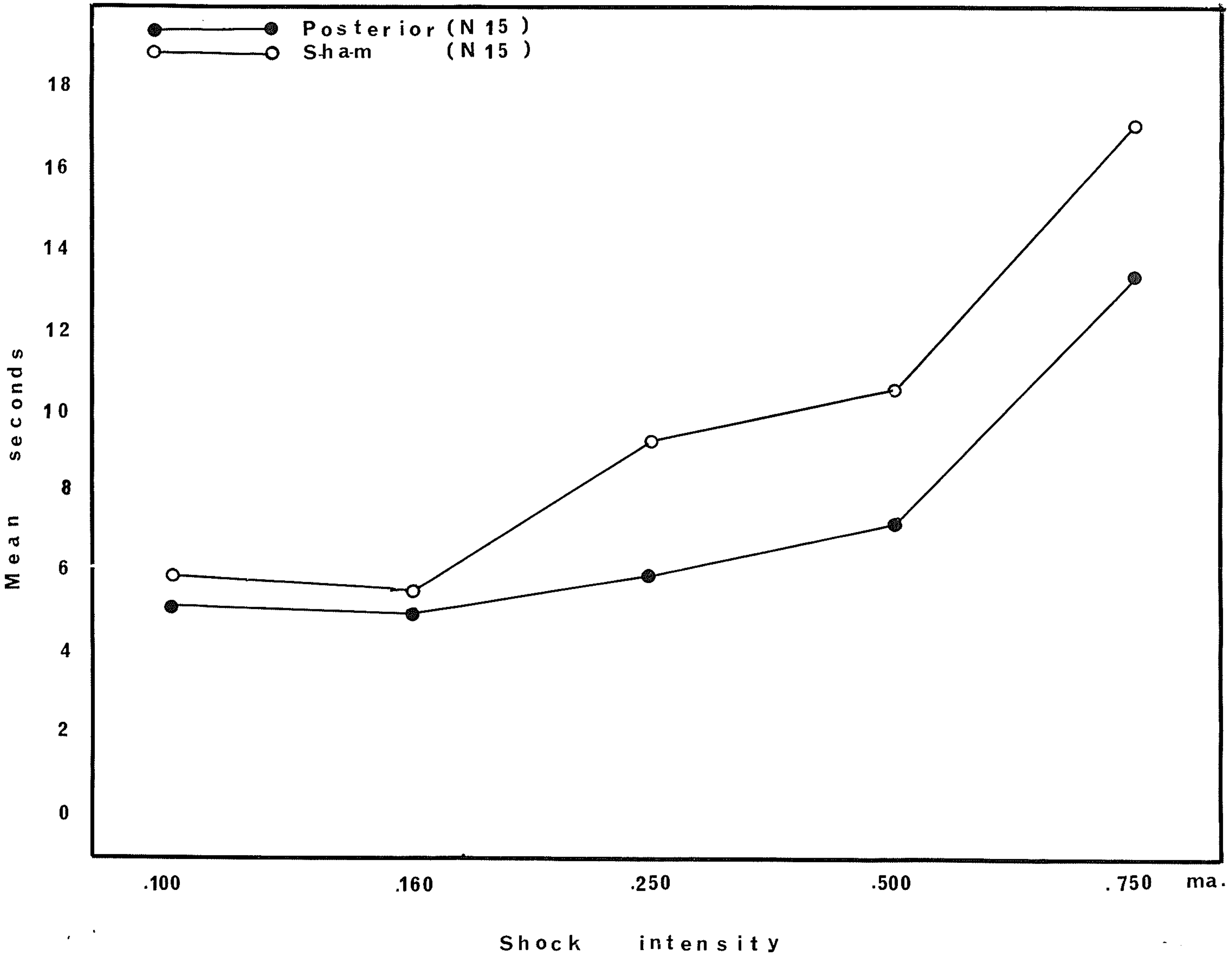

Figure 16. Passive avoidance running speeds from start to goal box

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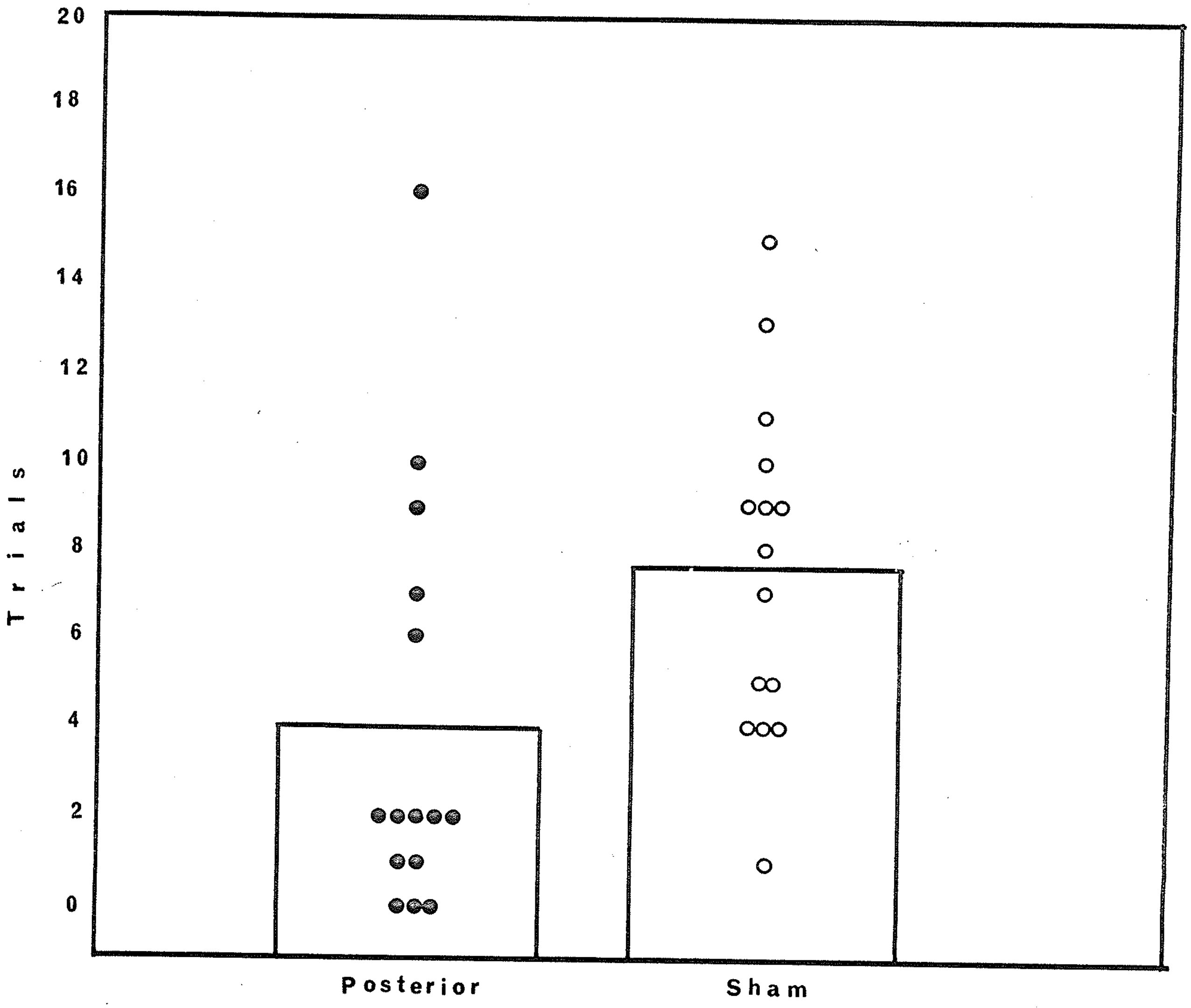

Figure 17. Passive avoidance, trials on which drinking was inhibited

Anatomical Results

Body and organ weights

Body weights were taken at the operation and at the end of the study. No significant group differences could be detected. At the end of the study Ss were prepared for histology in the same manner as described for Study I. No significant differences between groups were observed in testes and adrenal weights.

Histological results

After the brains had been hardened and cut, every 6th section was saved, except for four brains which were cut saggitally, and for which every 10th section was saved. Tissues were stained with the Klüver and Barrera cell and fibre stain. Lesions were reconstructed on Lashley-type diagrams and are presented in Appendix B. The lesions are similar to those described previously and it is apparent that in the majority of animals area 17 was completely removed.

TABLE XVI

SUBCORTICAL DAMAGE IN POSTERIOR LESIONS

	TYPE OF LESIONS					
STRUCTURE	SMALL		MEDIUM		LARGE	
	unilat.	bilat.	unilat.	bilat.	unilat.	bilat.
Head of caudate	# 62	-	-	-	-	-
Alveus	# 62	# 63	-	-	-	-
	# 65	-	-	-	-	-
	# 60	-	-	-	-	-
	# 48	-	-	-	-	-
	# 64	-	-	-	-	-
Hippocampus	-	-	# 58	# 53	# 59	-
	-	-	# 62	# 59	# 49	-
	-	-	# 46	--	-	-
	-	-	# 49	-	-	-
	-	-	# 57	-	-	-
	-	-	# 58	-	# 59	-
	-	-	# 60	-	-	-
	-	-	# 60	# 53	-	-

Table XVI summarizes the type of subcortical involvement observed for the various animals.

CHAPTER IV

GENERAL DISCUSSION

All striate rats, which had been operated as adults, were found to have difficulties with tasks in which the critical stimuli were visual. These findings may be regarded as constituting further evidence for Klüver's (1942) contentions that striate animals respond to visual stimuli on the basis of luminous flux, and that such lesions are likely to affect all visual behaviors. However, early lesioned animals were only impaired in the performance of some tasks, while for others their behavior was nearly normal. In some instances where differences between the early and late groups were observed, they were differences in degree, while for other tasks they were differences in kind. For example, all posterior groups made more errors in learning a brightness discrimination when ambient levels of room illumination were raised; however, the early group made fewer errors at lower levels of illumination than the late group. In contrast to the above, early lesioned _S_s responded like normal animals in the visual cliff test, while late lesioned _S_s were not able to respond normally. These findings were supplemented by further data for a visual cliff-type task. Here _S_s were put on a raised platform and their responses to the deep and shallow sides were studied. Again differences between early and late operates were found which suggest that early striate removals do not abolish perception. The performance of early operates on all other tasks suggests that these animals are visually impaired and respond on the basis of luminous flux. However, such interpretation does not apply to the visual cliff and related data. Other findings, to be discussed later, suggest that the performance of these animals in most tasks could have been impaired for other reasons. The data from the visual cliff-type tasks support the hypothesis that early damage to central sensory systems is less detrimental to recovery of function than similar damage incurred at maturity. In this respect our results are in agreement with those in the literature (Doty, 1961; Scharlock et al., 1963; Stewart, 1964; Wetzel et al., 1965). In detail, however, our results are at variance with the results of those investigators who found that visual pattern discrimination performance is not impaired by early lesions (Doty, 1961; Wetzel et al., 1965). As responsiveness to visual patterns is necessary in both types of tasks, our results for these two test situations will have to be reconciled, and the differences between our results and those of Doty and Wetzel have to be explained. Possible explanations will be considered after a discussion of the observed non-visual effects.

A variety of non-visual effects were found, some of which could have been responsible for the impairments on performance of visual tasks. Striate animals are impaired in avoidance behavior,as they had difficulties in both active and passive avoidance. In a great number of our experiments, which were designed to test the visual ability of the animals, shock was used to motivate the animals, it is, therefore, important to inquire further into the nature of such avoidance deficits. We performed a number of experiments which represent a first step towards an enquiry into this problem. We found that posterior Ss responded with startle and vocalization at higher levels of shock intensity than the shams when shock was applied to the feet and to the tail, although no differences could be detected for the tailflick response.

These findings, as well as the observations that shock avoidance deficits persisted throughout the various experiments and were independent of the age at which the operation was performed, suggest an affective change as a result of striate area removals which must interact in a complex fashion with the well-known perceptual deficits resulting from this kind of lesion. Such affective changes could be a result of changes in the visual stimulation, due to the change from normal to luminous flux vision. On the other hand, there is evidence that deficits in avoidance learning may occur without detectible deficits in visual discrimination performance. Lubar (1967) found that small striate lesions, which did not interfere with pattern discrimination, impaired shuttle-box avoidance learning. Such affective changes are likely to be more pronounced after massive lesions, and may affect the manner in which an animal will respond to visual stimuli even when visual capacity has recovered, as it may after early lesioning. In such a case a _S_ might have difficulties learning a pattern discrimination, not because of a loss of pattern vision, but rather because of a changed affective reaction to visual and noxious stimulation. Such affective changes are probably more important than has been acknowledged up to now. First, a great number of investigators have evaluated the effect of striate lesions on vision, using a Yerkes-type discrimination apparatus and shock motivation, without reporting any observations on avoidance behavior. Secondly, there is recent evidence that drugs known to change avoidance behavior also alter performance in visual tasks after striate lesions.

The loss of a preoperatively learned brightness discrimination, as a result of striate areas removal, has often been considered to be due to a memory loss, or loss of the engram for the habit. However, Braun et al. (1966) discovered that amphetamine treated striate rats would show savings in relearning such a task. Furthermore, Krieckhaus (1965b) found that amphetamine reduced freezing and improved avoidance performance. We feel, in view of the findings that amphetamine treatment, avoidance behavior, and postoperative brightness discrimination performance are interrelated in some complex fashion, that for other studies where loss of engram, losses of learning capacity and losses of sensory function are inferred, better explanation could be obtained by a study of affective changes after striate removals, and their role in the particular behaviors under study.

Another non-visual effect observed was that all posterior Ss were deficient in discrimination reversal, but early operated Ss were superior to later lesioned ones. Such data agree with those of Tsang (1936) and Lashley (1943) who ascribed some complex, non-sensory function to the visual cortex, which is less impaired by early lesions (Landsdell, 1953).

With regard to our main objective, the comparison of late and early removal of striate areas, as it affects visual behavior, the most puzzling finding was that while early Ss were unable to learn the pattern discrimination they responded like normals in the visual cliff. It would be naive to expect no visual deficits at all after early brain damage. Study of our Ss' behavior, when put on an elevated platform, showed that deficits are noticeable even in a visual cliff-type situation. Nevertheless, it is surprising that, even after having received three times as much training as the controls, early posteriors made no differential responses to visual patterns in the Yerkes-type apparatus.

It is possible to argue that early resection of visual areas impairs only some aspects of pattern vision, such as those important in pattern discrimination, while leaving intact others, such as those necessary to respond in the visual cliff. It seems more reasonable, however, to assume that recovery of function after early lesions should be general enough to be detected in a wide range of behaviors which are likely to require similar visual capacities.

In trying to account for these findings, methodological differences between our study and those reported in the literature are important. Both Doty and Wetzel raised striate cats in an enriched environment whereas our rats were raised under 'normal' laboratory conditions. Landsdell (1953), Smith (1959, and Schwartz (1964) have shown that the effects resulting from early posterior cortex removal depend very much on the type of environment to which the animals are exposed after the operation. The hypothesis that striate rats, lesioned at birth, will recover the ability to perform pattern discrimination seems, therefore, reasonable and should be investigated experimentally.

The present study differs also from those of Doty and Wetzel in that animals of a different species were used. There are several indications that species specific differences exist between cats and rats after lesions in the central visual system. Blake (1959) found that lesions of the superior colliculi interfere with pattern discrimination; there is no evidence which shows that collicular lesions would abolish pattern vision in the rat. Meyer (1966) found that striate removal in mature rats would abolish visual cliff behavior, whereas it had no such effects in cats. Although Meyer's cats had incomplete visual cortex removals, and only a very small number of animals were used

used, phylogenetic differences between rat and cat could account for many of the discrepancies discussed. The evidence would support the idea that vision is more dependent on the cortex in the rat, whereas in the cat subcortical centers, like the superior colliculi, can adequately function in complex visual behaviors. Already Klüver (1942) suggested that the principle of encephalization may not apply to development of vision in various species of higher and lower animals. It is possible, therefore, that the superior colliculi have a more important function in vision in the cat than in the rat. In this connection it is of interest to note that striate cortex removal in the tree shrew does not abolish pattern vision. Polyak (1957) points out that tree shrews have very well-developed colliculi, which are, therefore, likely to be even more important than the striate areas. Unfortunately, little is known about collicular function in the cat and nothing is known about the colliculi in rat. Further research into such problems will likely unearth important new facts which will answer some of the present questions.

A major problem in evaluating the effects of specific brain lesions on specific functions, such as vision, is that most experiments are designed with little regard for ethological considerations. For example, rats' and cats' performance is compared in a similar task and with similar lesions, without any knowledge about the function of vision in the normal animal in its natural environment, and the meaning of particular types of visual stimuli have for an animal. Considerations of this nature will lead to more natural testing situations in which it will be easier to obtain valid information of the visual capacities of various species.

Further, we believe that our study emphasizes the desirability of a multi-dimensional approach to problems of evaluating behavior after brain lesions. Rather than using a single measure and a single task it is important to study an operated animals' responses by a variety of measures and in different tasks. While it is apparent that such an approach will not always yield simple and unambiguous answers, it may lead to new insights into complex brain-behavior relationships.

In summary, we have shown that early and late visual cortex removals in rats result in a variety of visual and non-visual changes in several behaviors. While early lesions allowed recovery of some functions, and were less deliterious to performance in some tasks, other deficits were found, the severity of which was not affected by the age of the animal at the time of operation. Although most of the experiments reported can be integrated with existing findings and explanations, if this study is considered as a whole it seems to preclude any simple explanation of the effects of striate lesions on behavior. Several possible explanations of the major findings were discussed and further experimental solutions to some of the problems were proposed.

SUMMARY AND CONCLUSIONS

The present investigators were concerned with determining the effects of neonatal and adult removal of the visual areas on the behavior of the rat. The obtained visual and non-visual data will now be summarized.

1. Light preferences were investigated in a straight runway, half of which was illuminated while the other half was kept in darkness. Two tests were given: one at 40 days of age after neonatal lesions, the other after a second operation had been performed in which half of the

previously sham operates had their visual cortex removed, while all other Ss were sham operated. The results for both tests indicated that striate removals decrease the rats' light aversion and that adult lesions resulted in a more pronounced effect than infant lesions.

2. Two visual cliff tests were given; one before and one after the second operation. It was found that early lesioned Ss performed like controls in that they preferred the shallow side of the cliff. By contrast, no such preferences were found in the later lesioned Ss. These results showed that early lesions may not inhibit the development of normal depth perception.

3. Brightness discrimination performance was studied in a Yerkes-type discrimination apparatus, with a white square as the positive and a black square as the negative stimulus. All Ss were able to learn the task and there were no differences between early and late lesioned Ss. All posteriors needed more trials and made more errors than the controls.

4. After having learned the brightness discrimination all Ss were trained on a pattern discrimination with a card bearing horizontal stripes as the positive stimulus and one bearing vertical stripes as the negative stimulus. Ss were trained to a criterion of 18/20 trials correct or a total of 200 trials. All posteriors were unable to learn the discrimination, regardless of the age of the lesioning.

5. To test the notion that striate rats perform on the basis of luminous flux cues, brightness discrimination performance was tested when the ambient level of room illumination was increased. It was found that the performance of all posteriors broke down at lower levels of illumination than that of the controls, and that early lesioned Ss were superior to later lesioned ones in maintaining performance at

lower levels of illumination.

6. As a further test of the animals' ability to respond to visual depth, Ss were put on a raised platform from which they could descend to either a shallow or a deep side. The height of the platform was systematically varied. It was found that early lesioned Ss responded in a manner which suggested that they were able to respond to depth, although their behavior differed from that of normal animals. The late lesioned Ss, on the other hand, seemed not to respond in a manner comparable to either the controls or early lesioned Ss, and their behavior was considered to support previous conclusions that these animals were not responding to visual depth.

7. All Ss were subjected to discrimination reversal training, in which it was found that posterior Ss made more errors to reach criterion than controls. Early lesioned Ss performed better than late lesioned ones. These results are in agreement with reports in the literature that the striate areas have a non-sensory function and are important in learning.

8. In addition to the observation that all posterior Ss were significantly more active than controls, it was found that in all tasks using the Yerkes-type discrimination box and shock motivation, they were impaired in shock motivation. These deficits were consistent for all tasks and no beneficial effects of early lesions were seen.

9. To investigate the notion that deficient shock avoidance behavior was reponsible for impaired performance of striate rats in the brightness and pattern discrimination, a new group of 60-day old animals were operated and tested in a brightness discrimination while they were injected with either amphetamine or saline. There were no

differences in the number of shocks received for the posterior amphetamine and saline treated groups, and all posteriors made significantly more errors than the sham operates.

10. Subsequently, the same animals' response to foot shock in an open field and to shock applied to the tail were investigated. It was found that all posteriors reacted with a startle response to foot shock at higher shock intensities than normals. There were no differences between posteriors and shams in the intensities at which tailflick occurred. In both situations, posteriors differed from shams in that higher intensities were needed to produce vocalization.

11. Lastly, passive avoidance learning was investigated at varying intensities of shock received through the spout of a water bottle in the goal section of a straight runway. It was found that posteriors were deficient in inhibiting their drinking responses and that they also had shorter latencies than the controls at some levels of shock intensity.

Several conclusions were drawn from these experiments. Neonatal removals of the visual areas were less detrimental to performance in several visual and non-visual tasks, while they did not differ in their effects from later lesions on the performance of other tasks. It is reasonable to assume that some aspects of pattern vision must have developed sufficiently in early lesioned rats to enable them to respond to depth in visual cliff-type situations. The failure to obtain similar findings for the pattern discrimination task could be due to several factors. It could be that those aspects of pattern vision needed in this task were selectively impaired by the operation. This suggestion was rejected, however, on the grounds that recovery of visual function after early lesions should affect visual behavior in a variety of situations. It is possible, however, in view of the findings that striate animals seem to have a changed reactivity to shock, that their inability to perform a pattern discrimination could have been due to the fact that they were trained using shock motivation. To explain the differences between our data and those from the literature it was proposed that phylogenetic considerations were important and that the inability of our animals to learn visual patterns could be due to a greater dependence of vision on an intact striate cortex in the rat. Lastly, methodological factors could have been responsible for our results, and it is possible that rearing in an enriched environment will reinstate pattern discrimination performance in the neonatally lesioned rat. The various explanations will have to be subjected to further experimental study. The results of our study support the contention that to evaluate behavior after brain lesions a multi-dimensional approach is needed, in which animals are tested in a wide range of different situations. It is hoped that an appreciation of the complexity of the effects of such lesions will result in fewer oversimplified generalizations.

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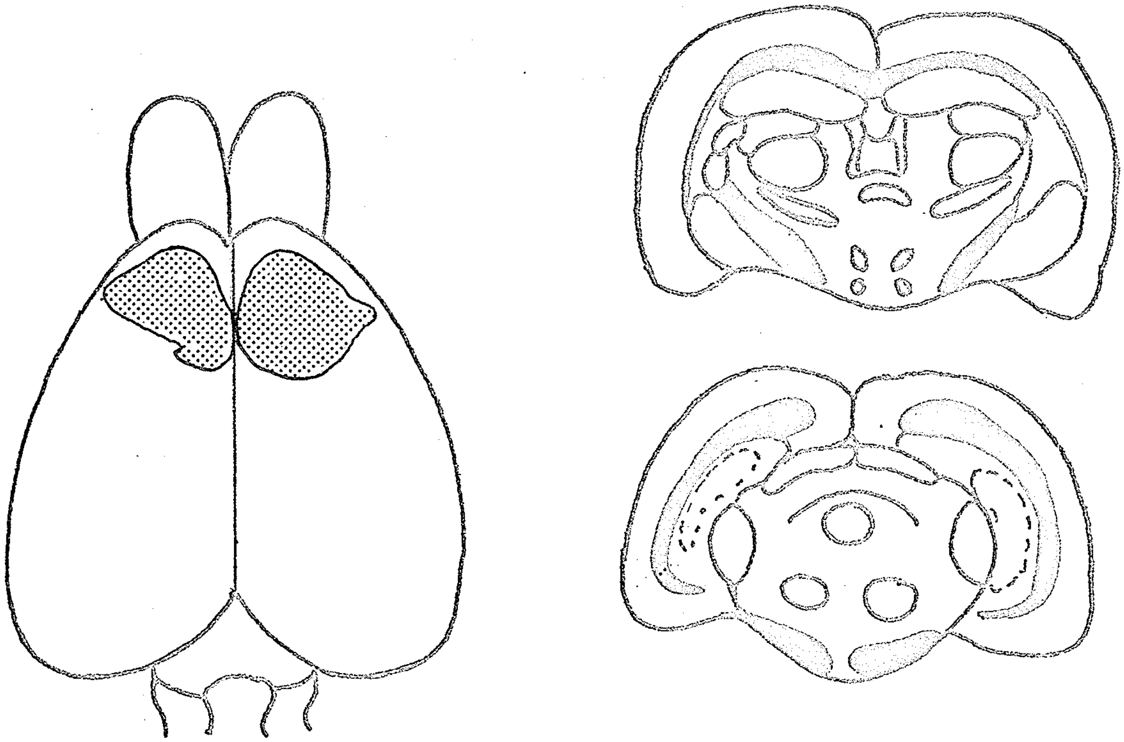
APPENDIX A

DIAGRAMS OF THE EXTENT OF INDIVIDUAL BRAIN LESIONS OF ANIMALS USED IN STUDY I



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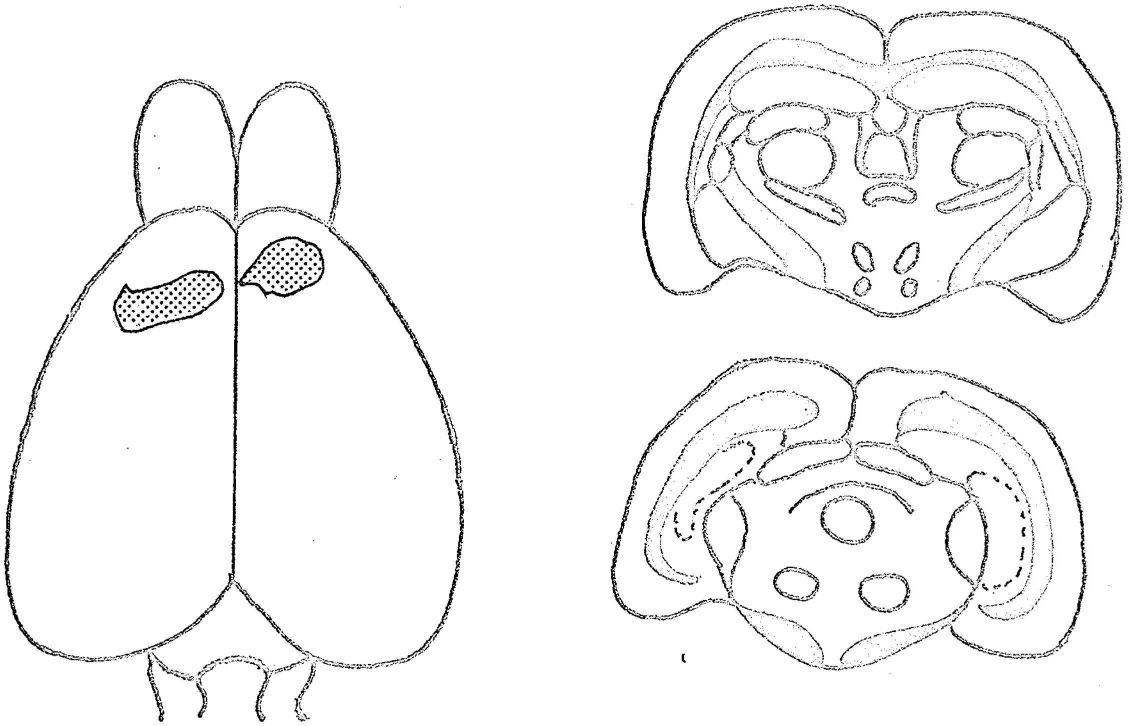

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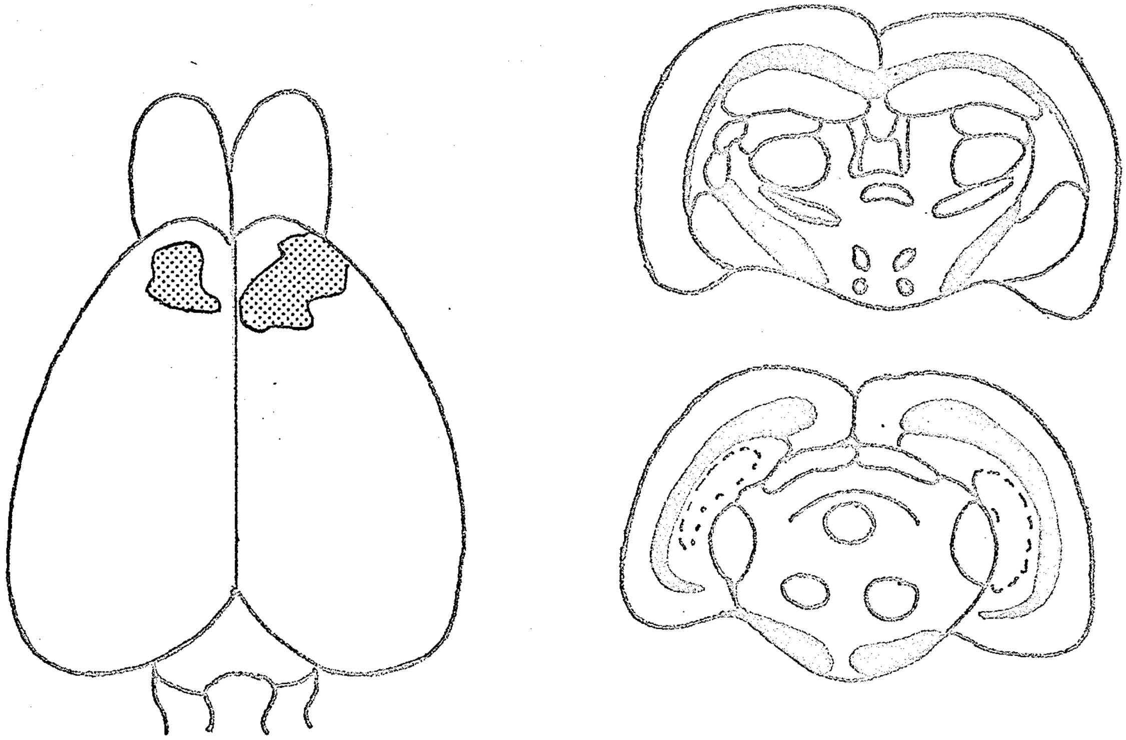

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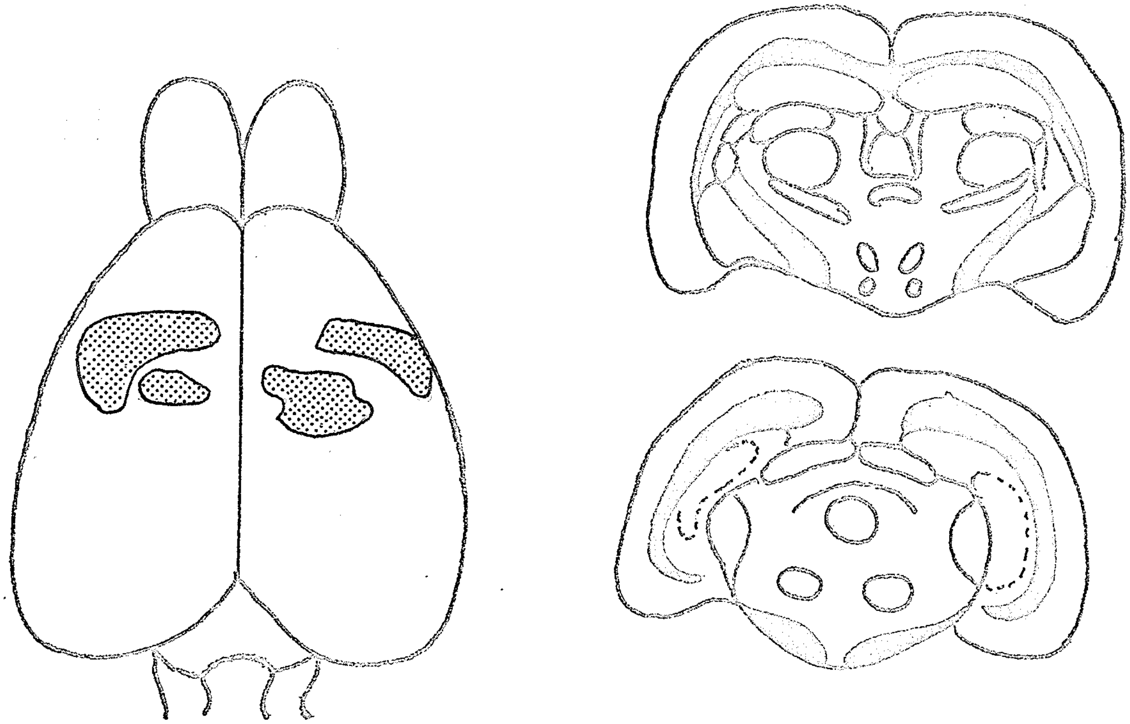

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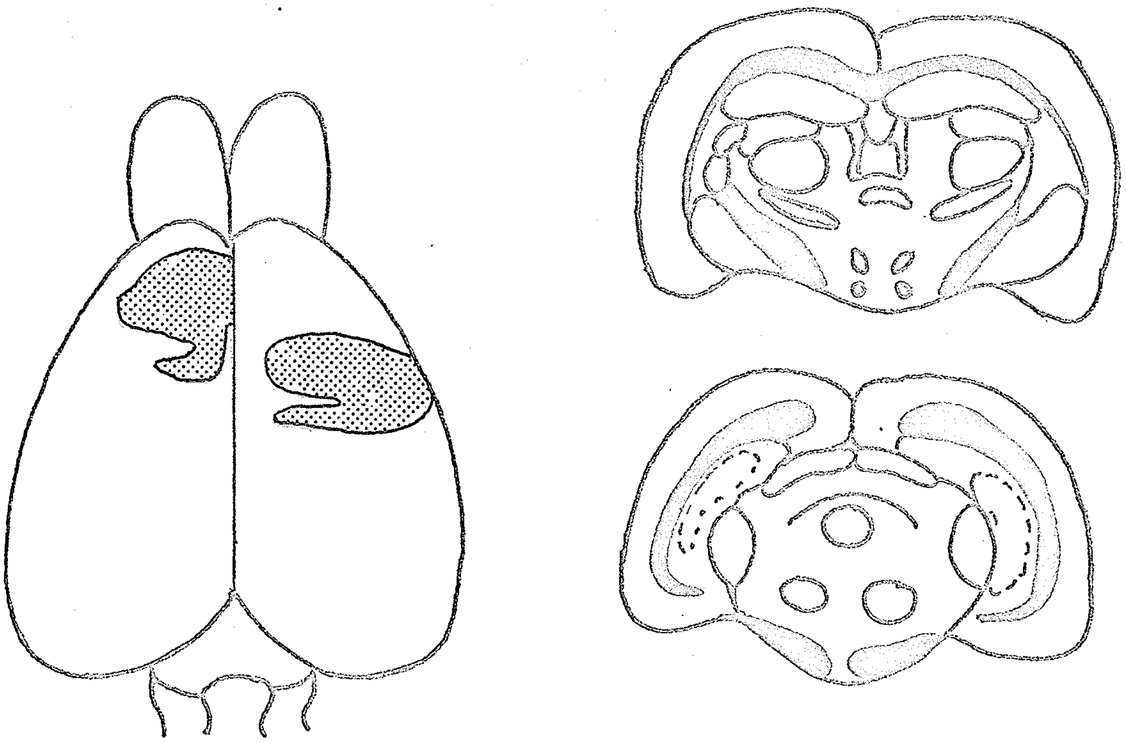

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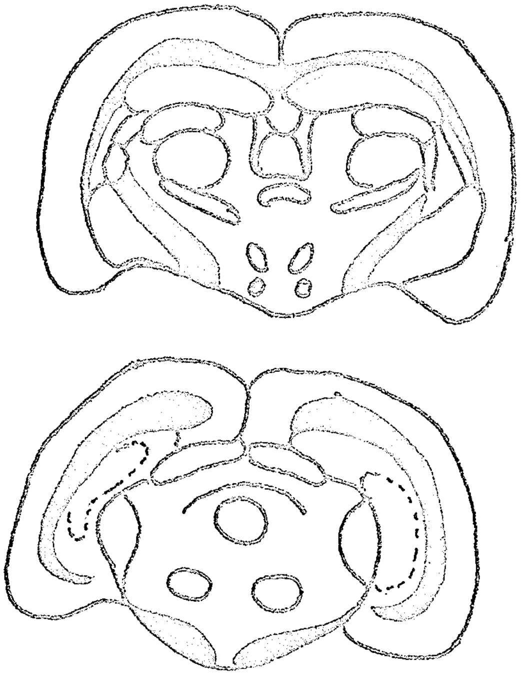

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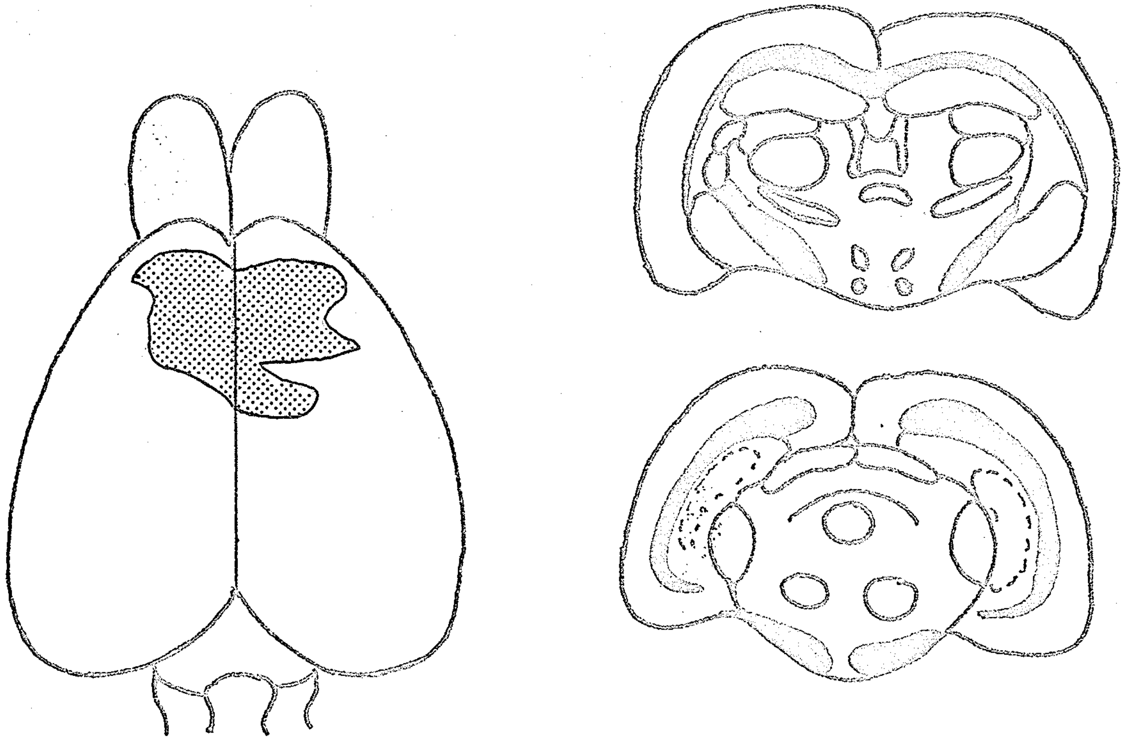

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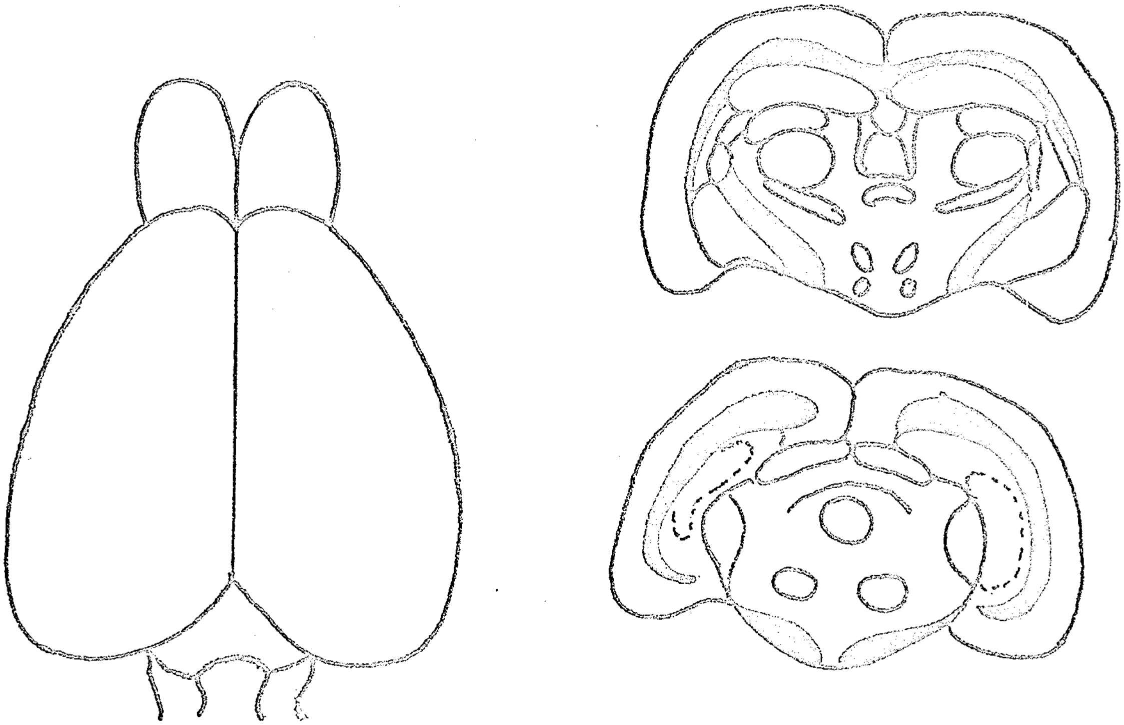

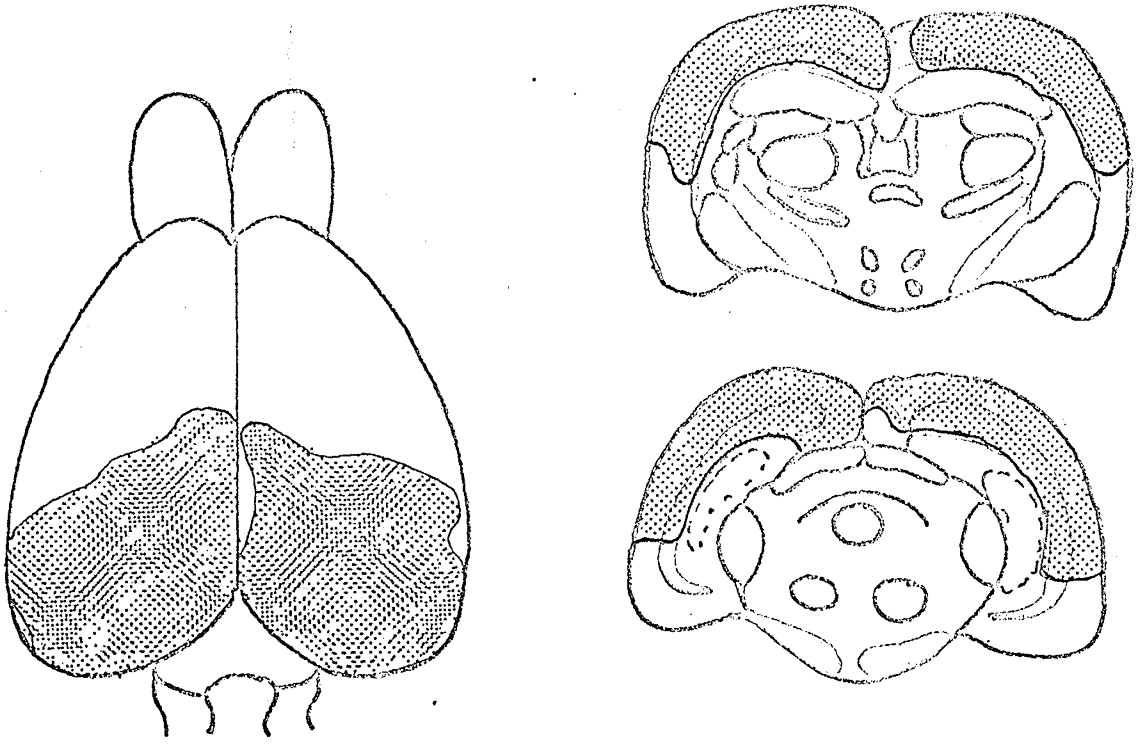

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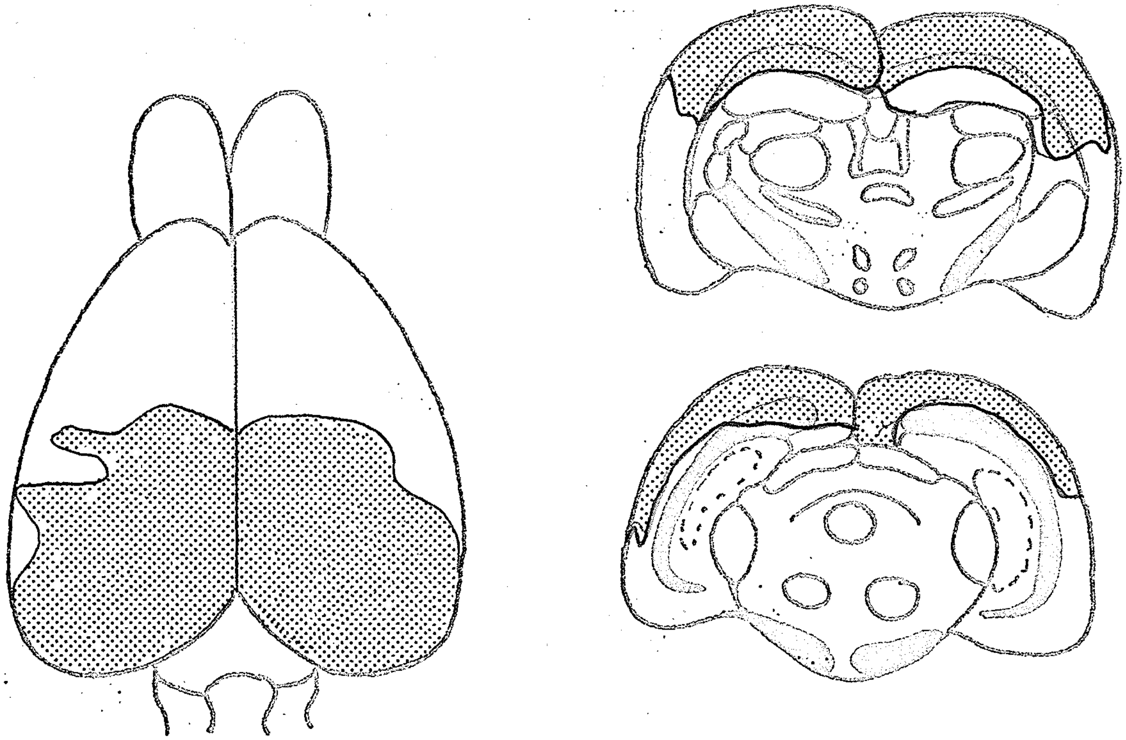
PS 3—5



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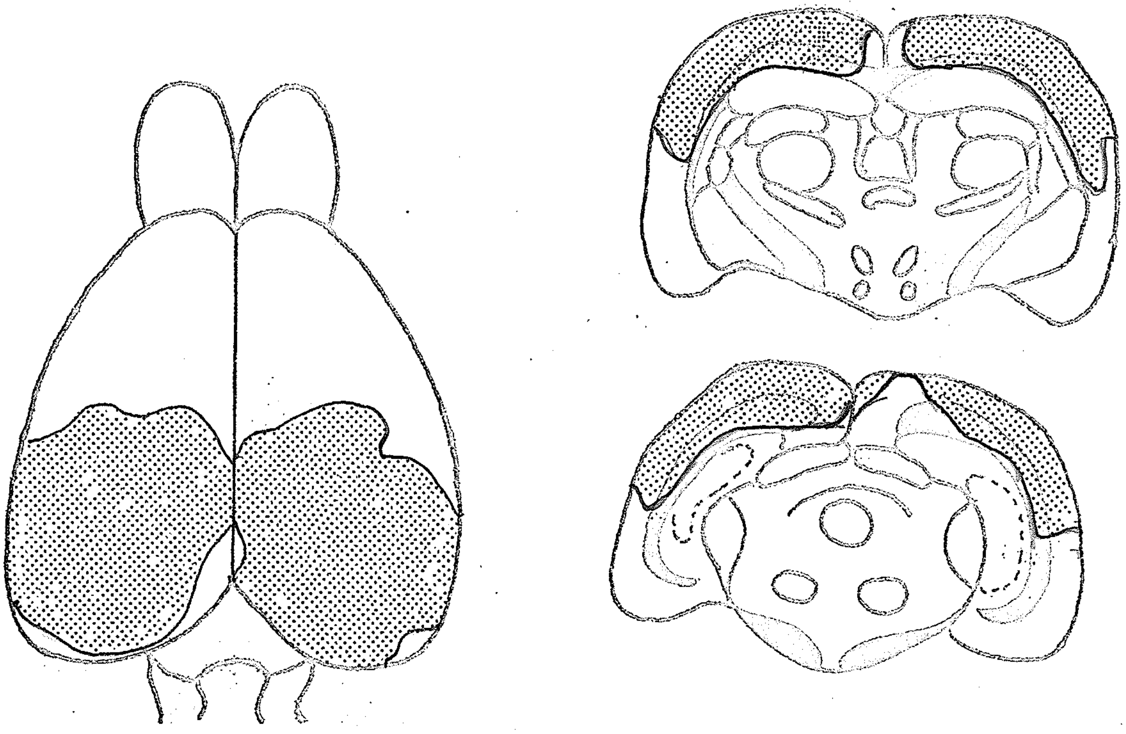

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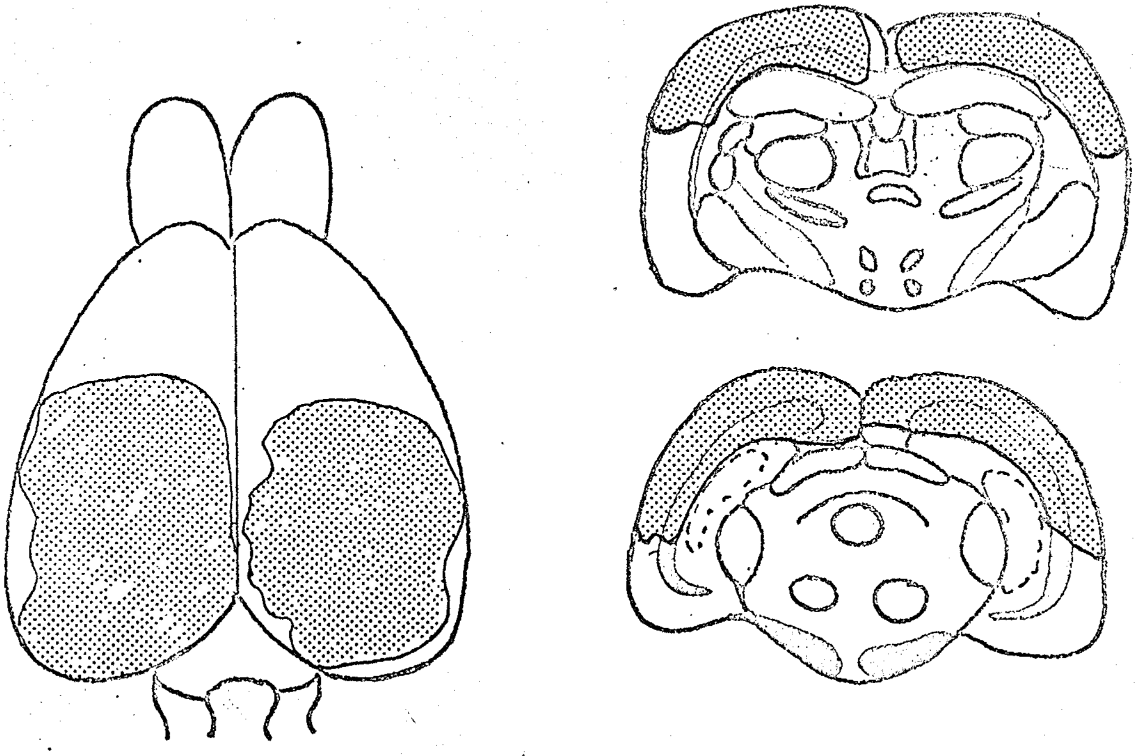

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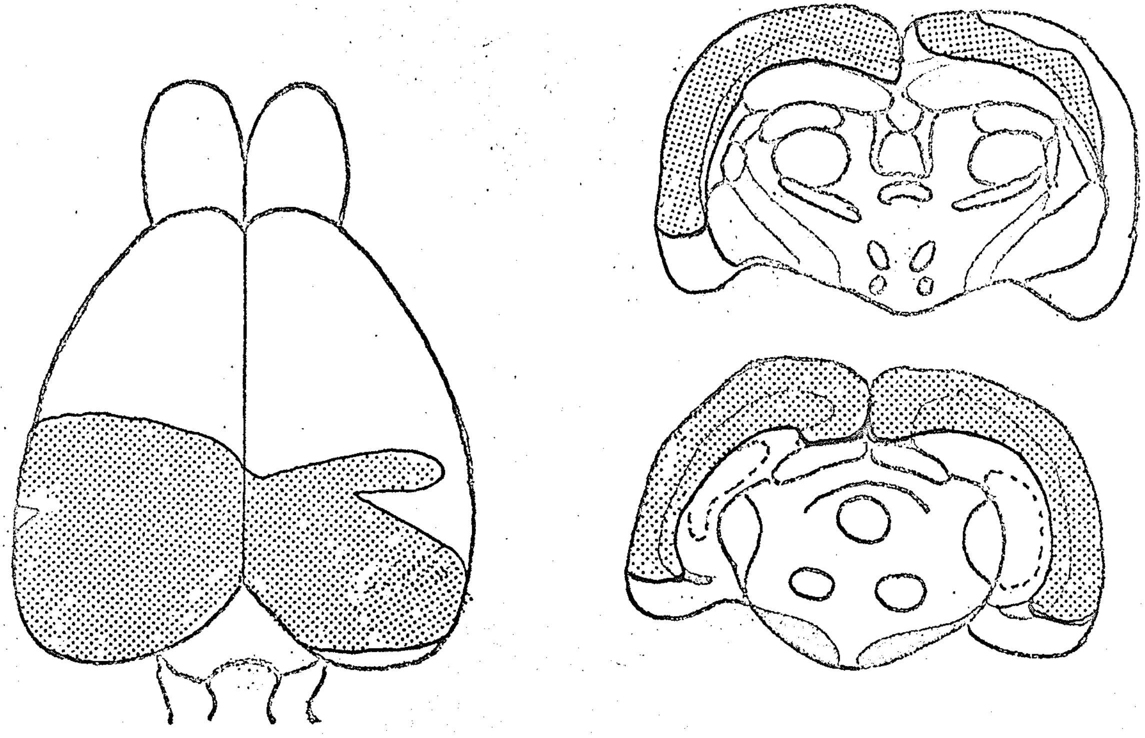

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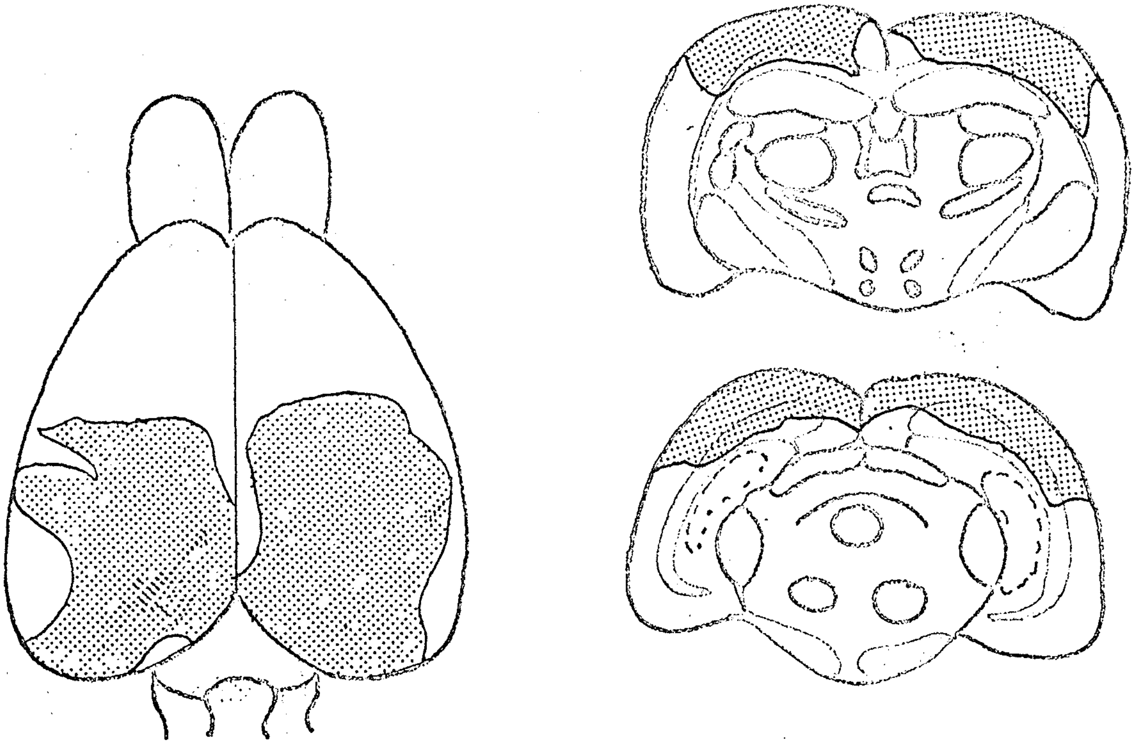

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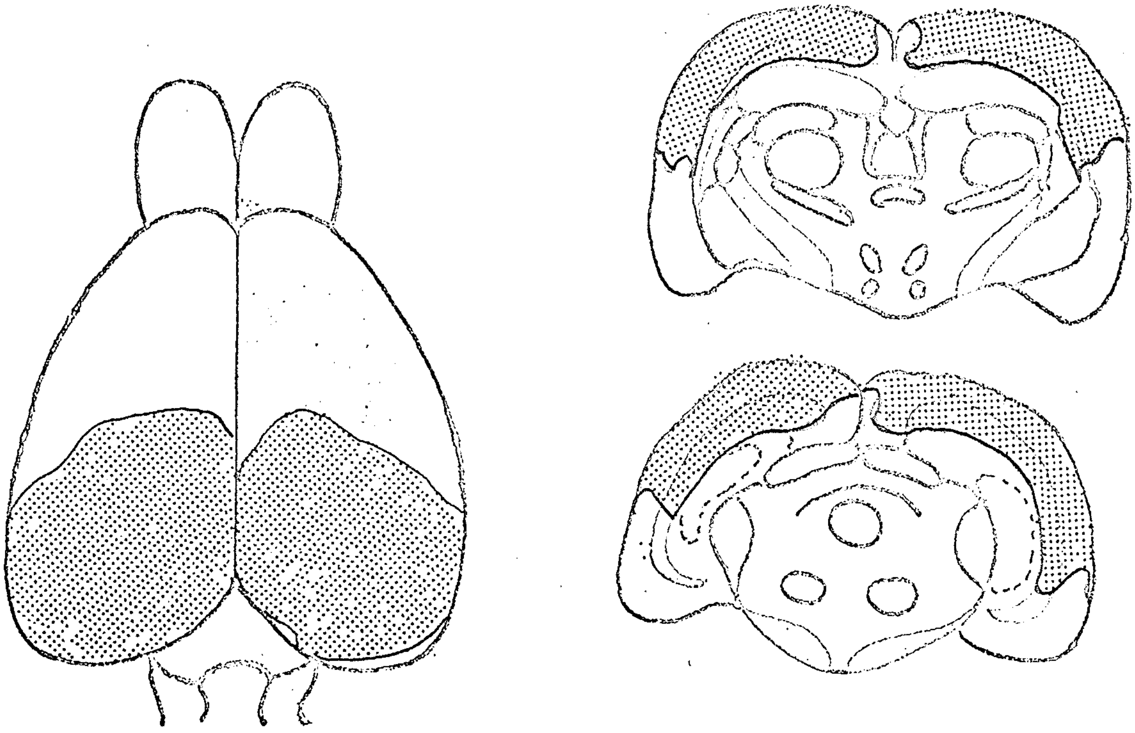

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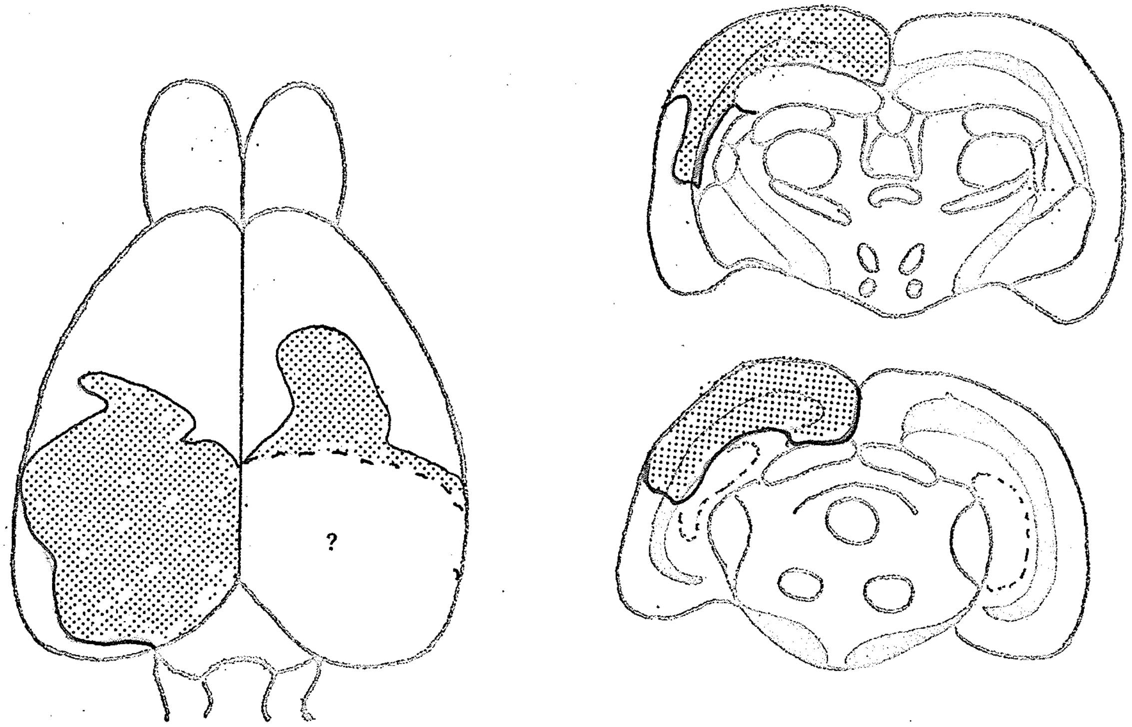

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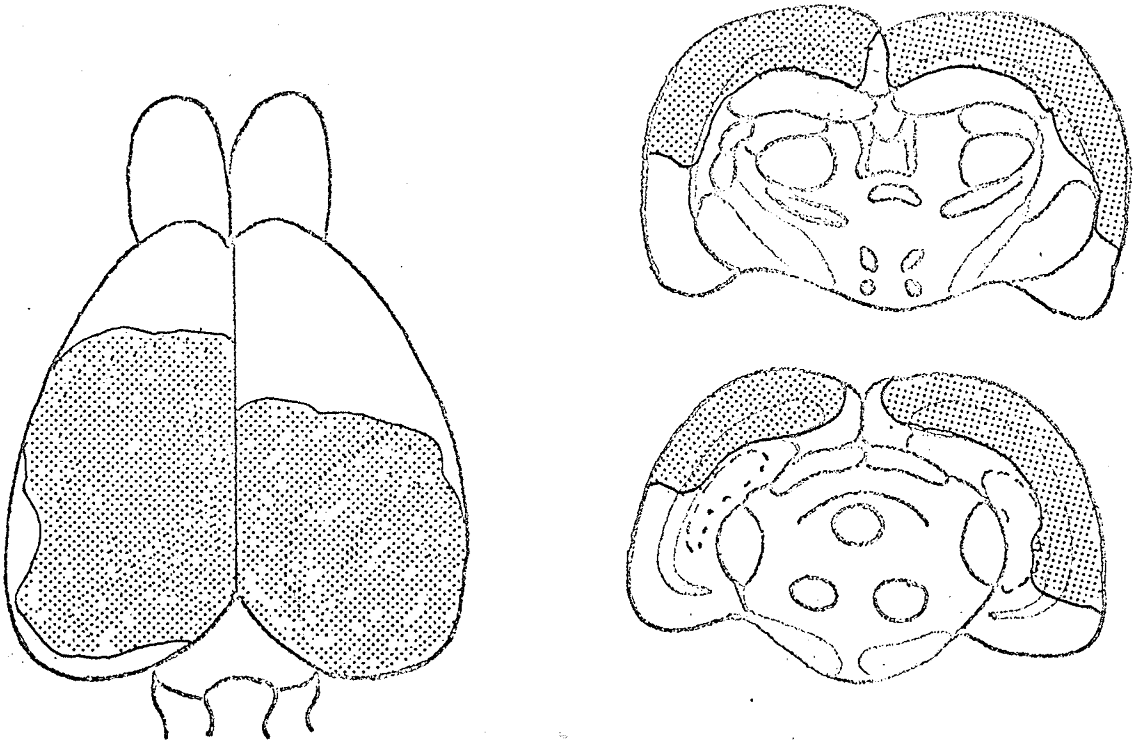

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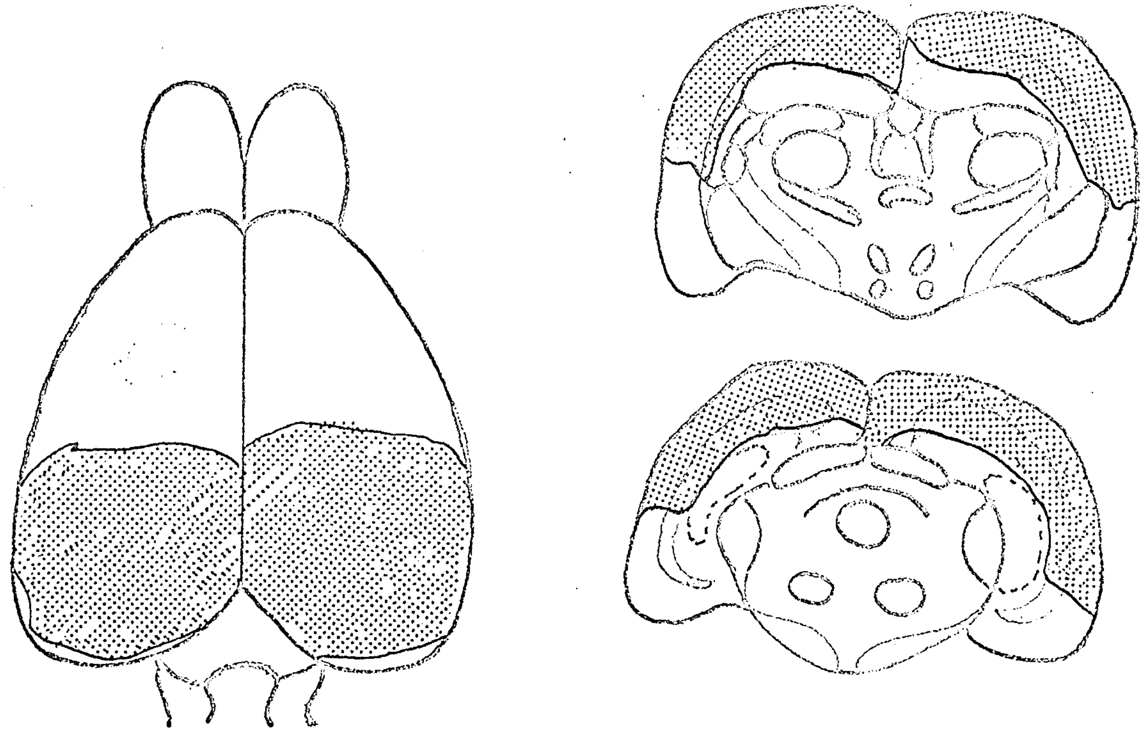

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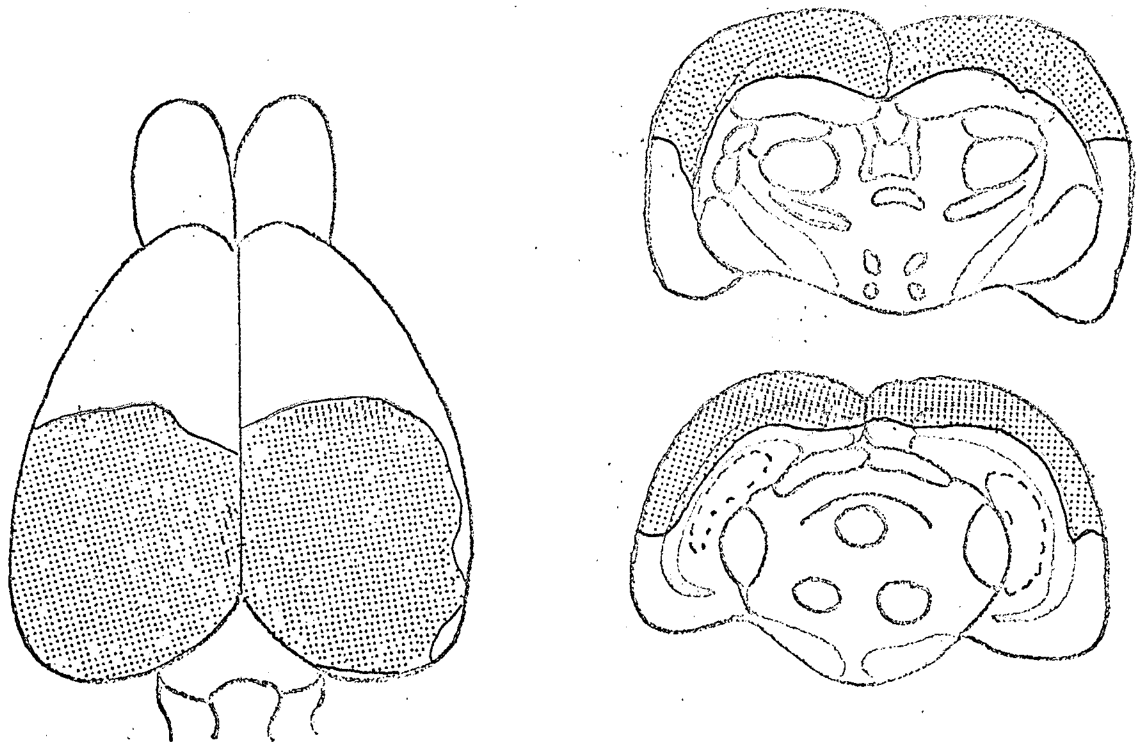

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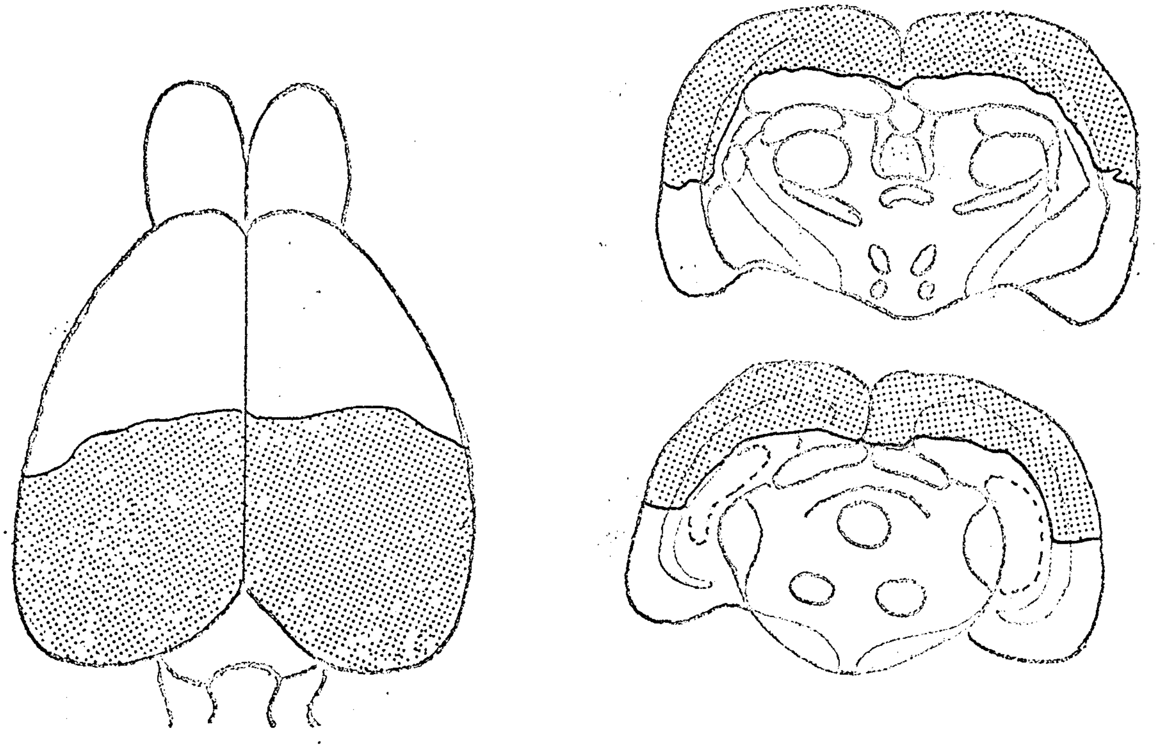

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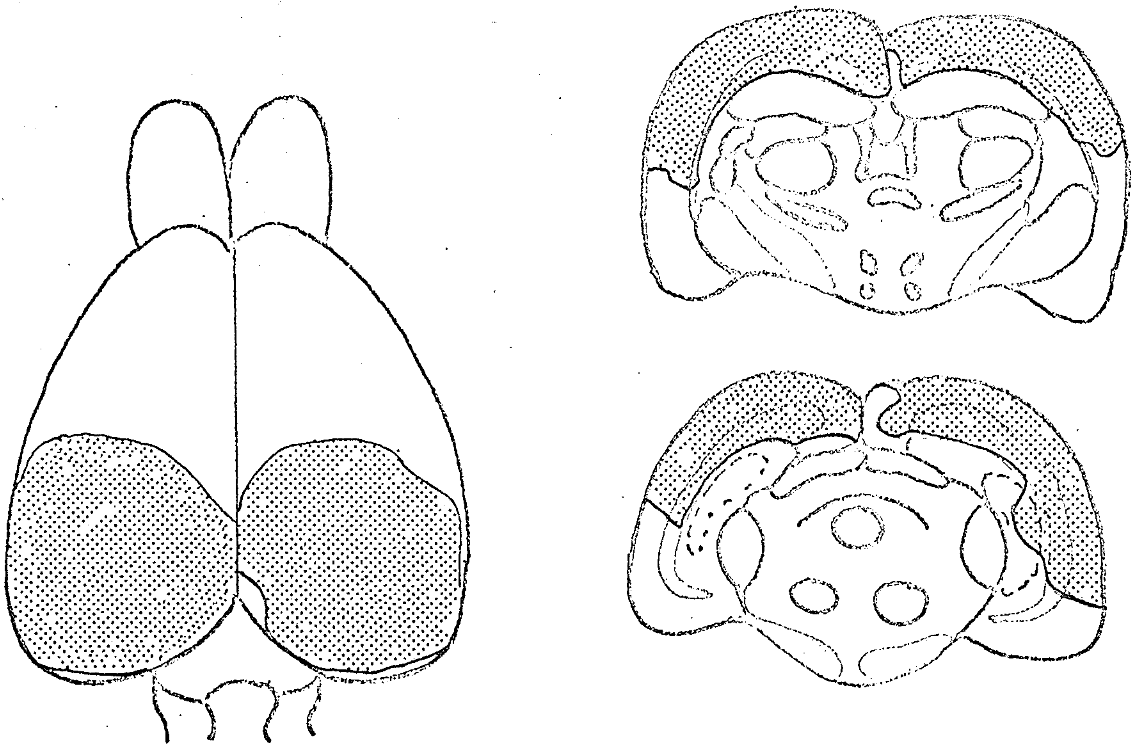

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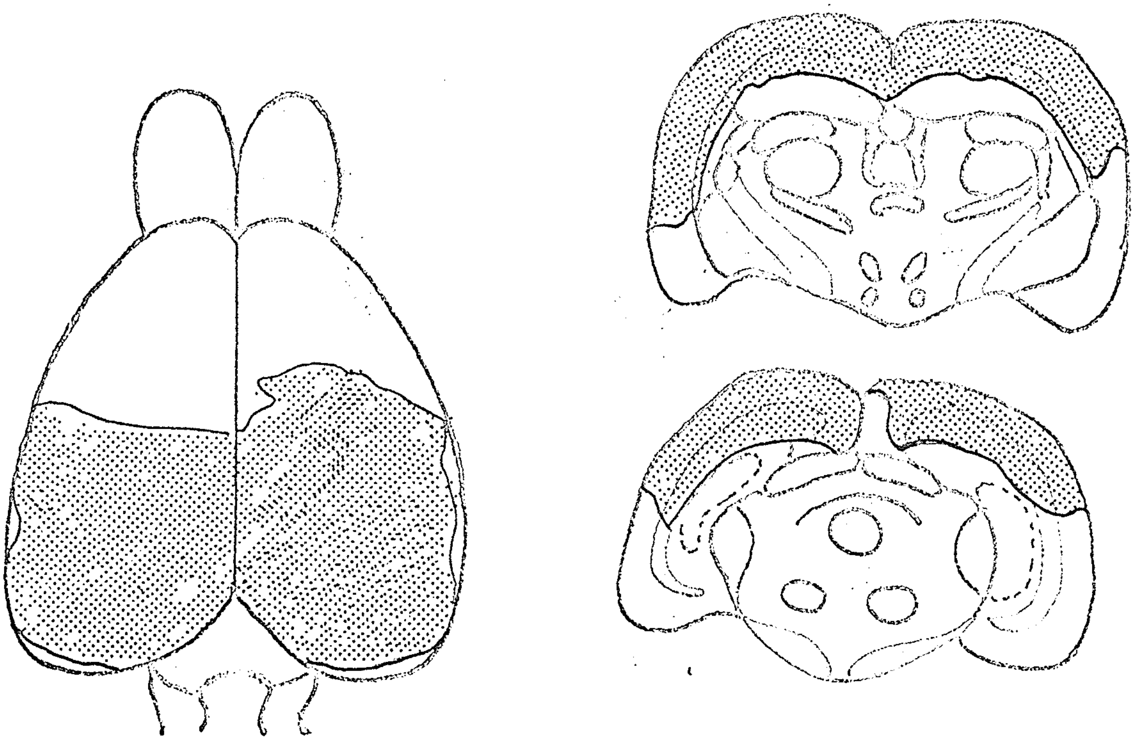

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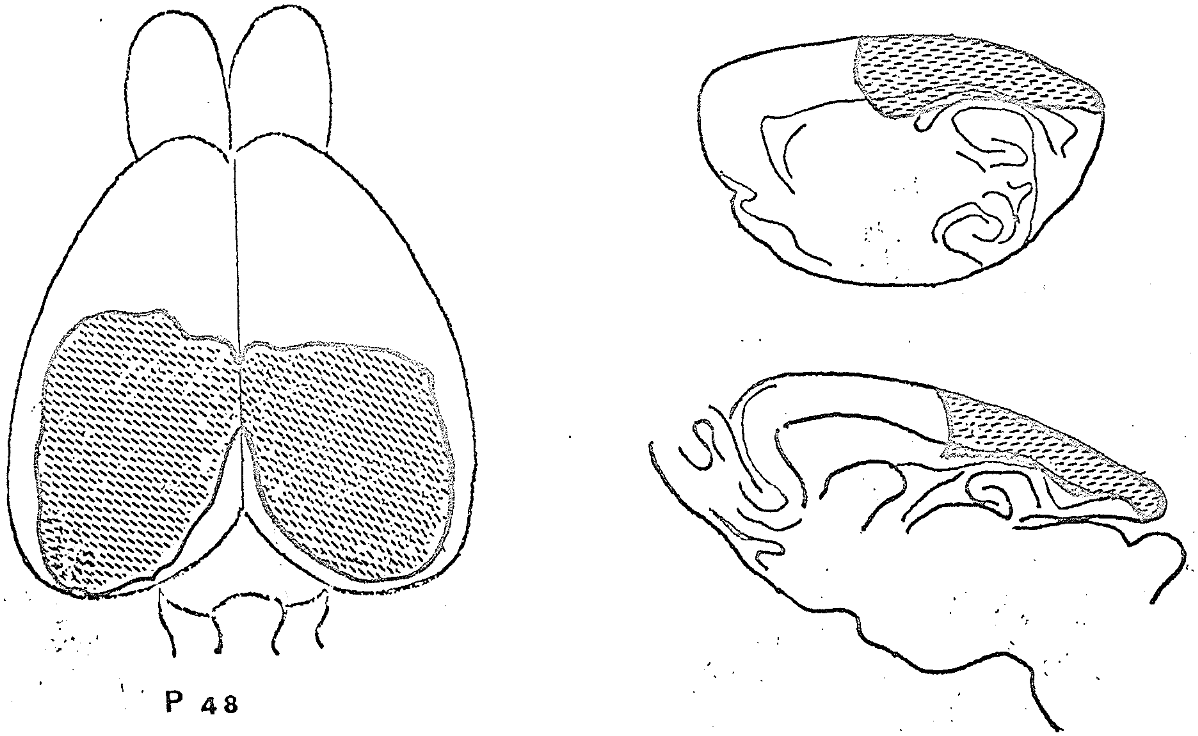
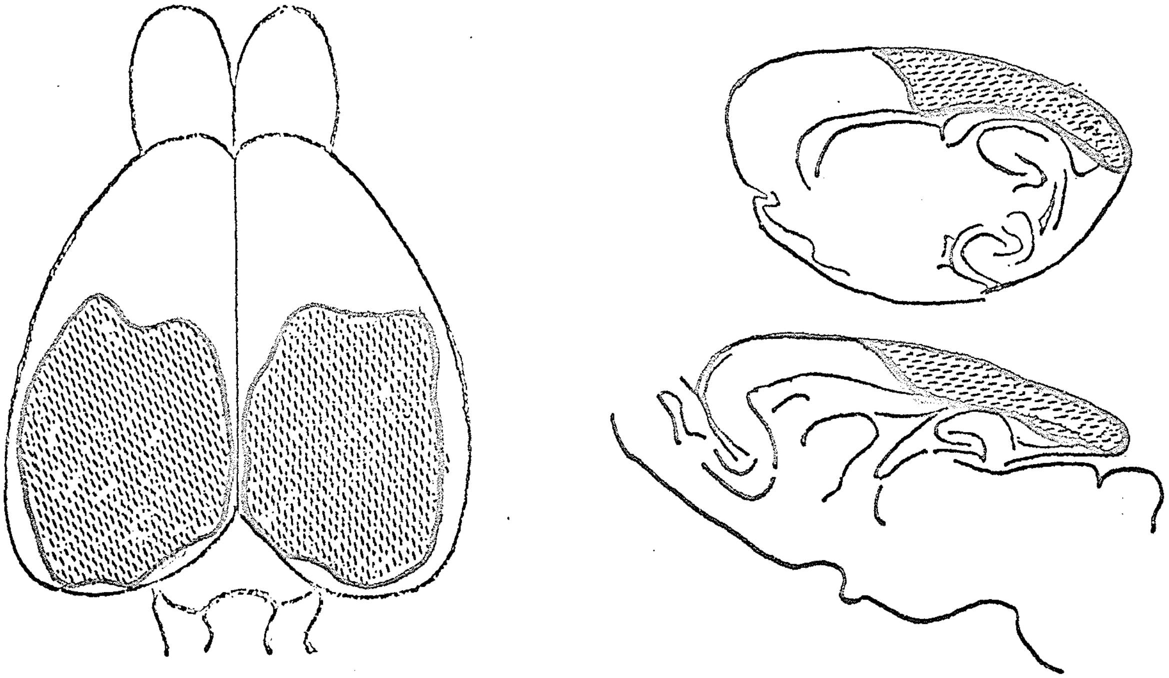
APPENDIX B

DIAGRAMS OF THE EXTENT OF INDIVIDUAL BRAIN LESIONS OF ANIMALS USED IN STUDY II



P 48



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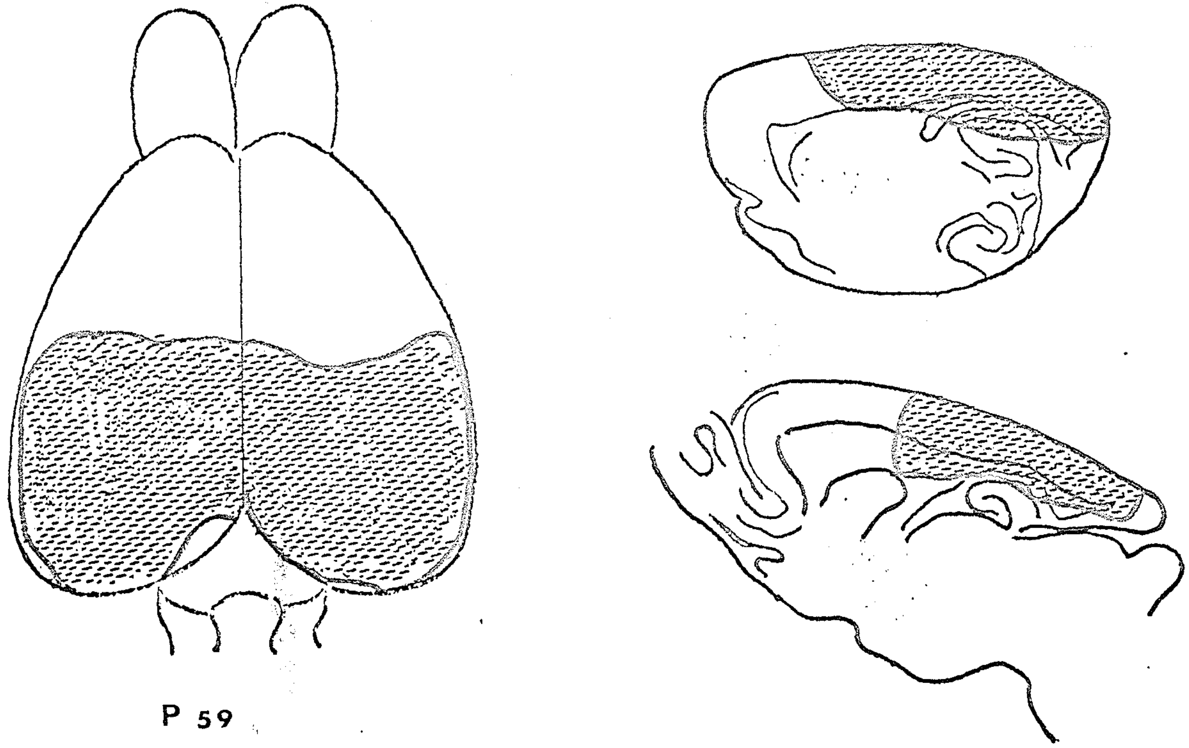

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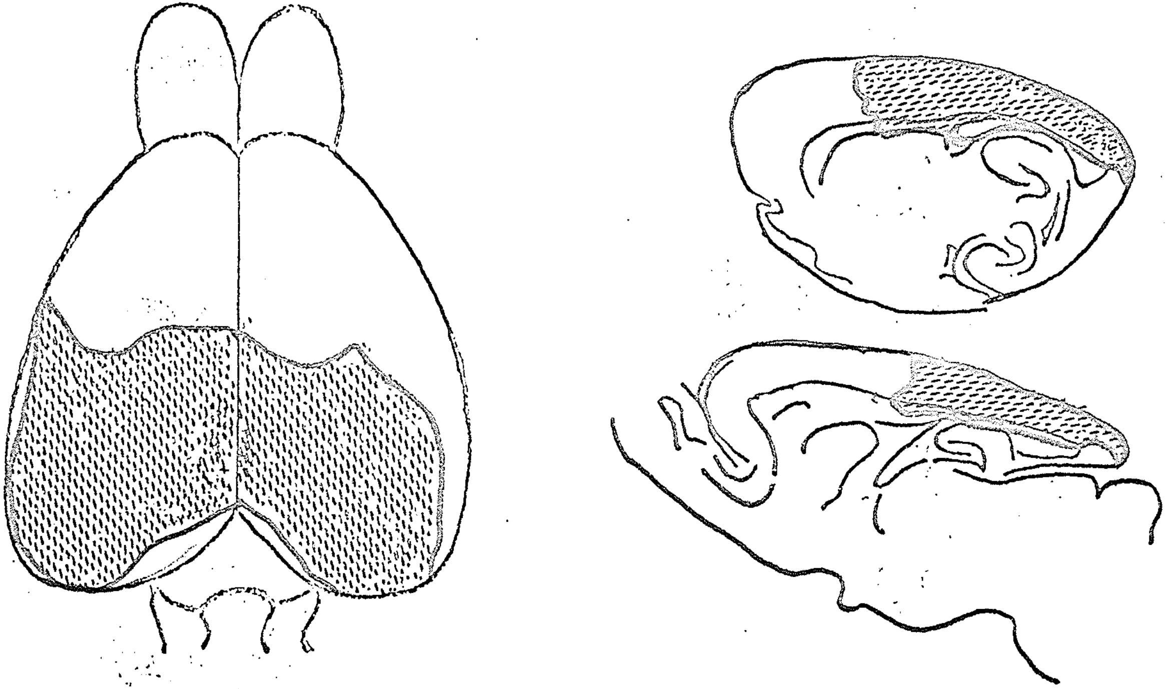

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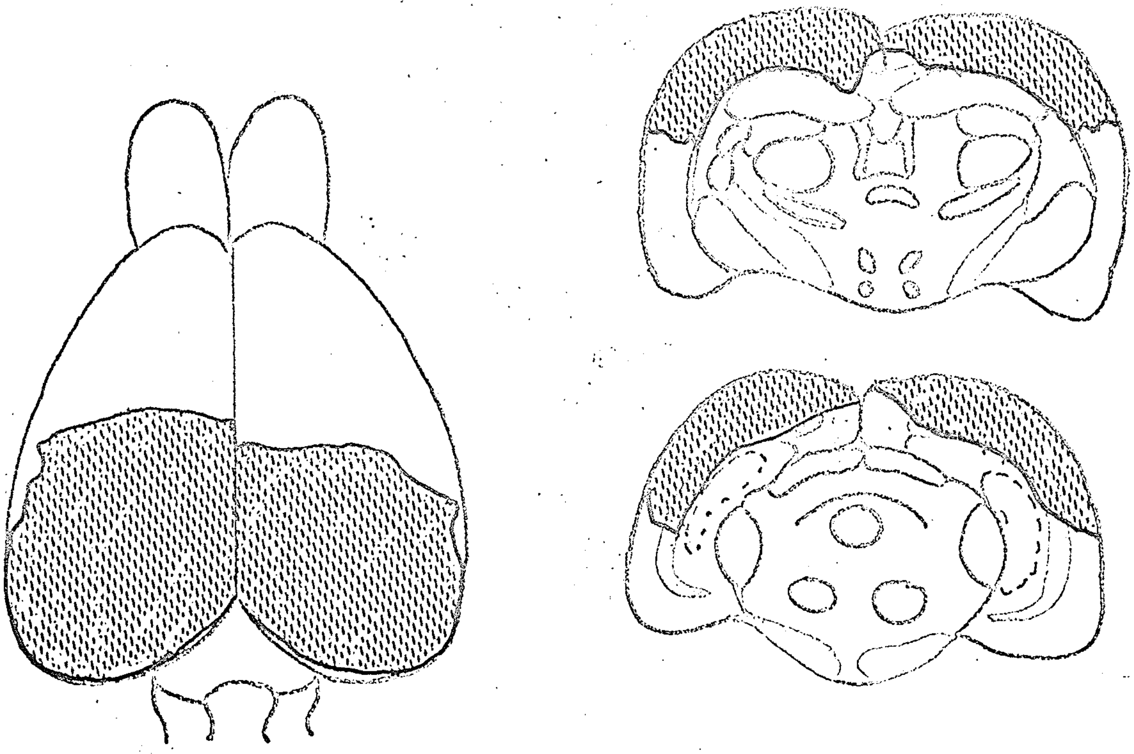

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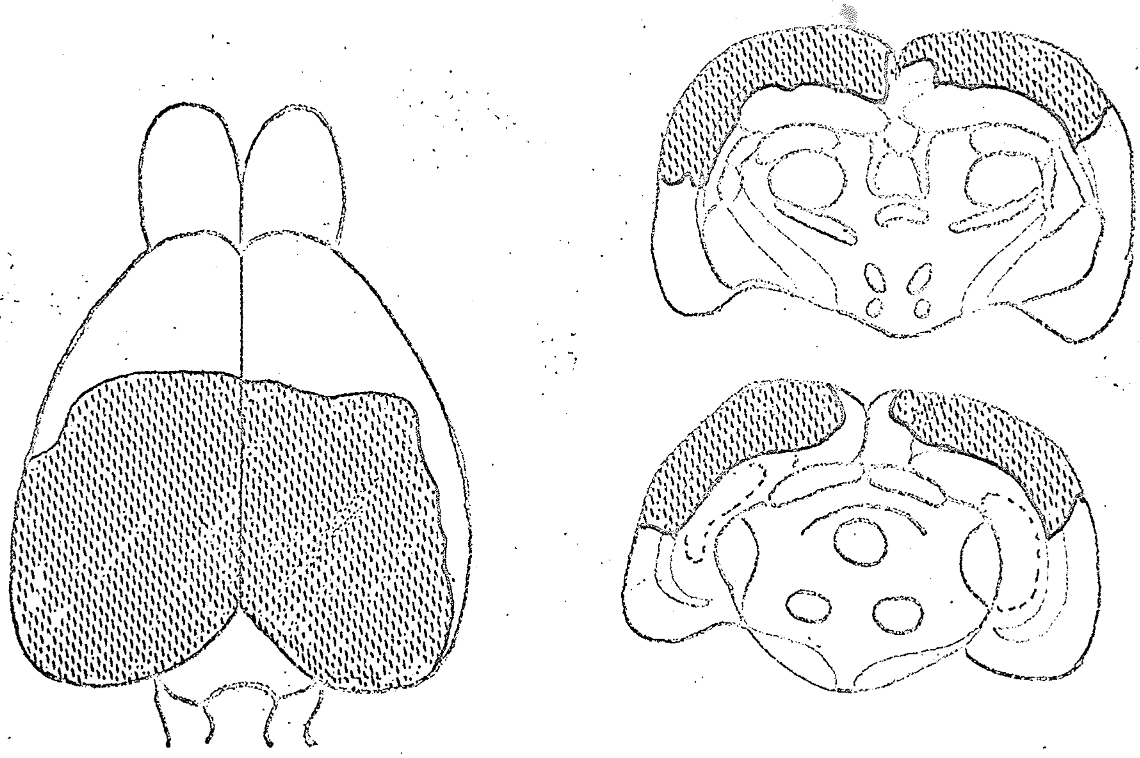

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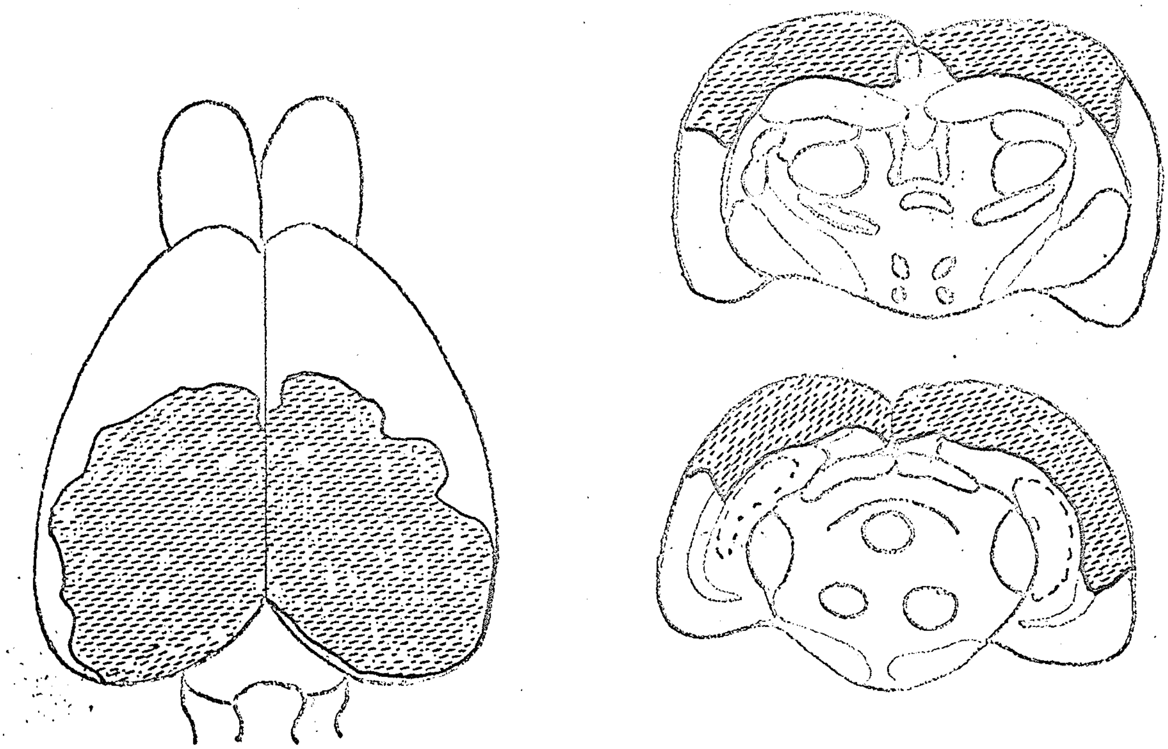

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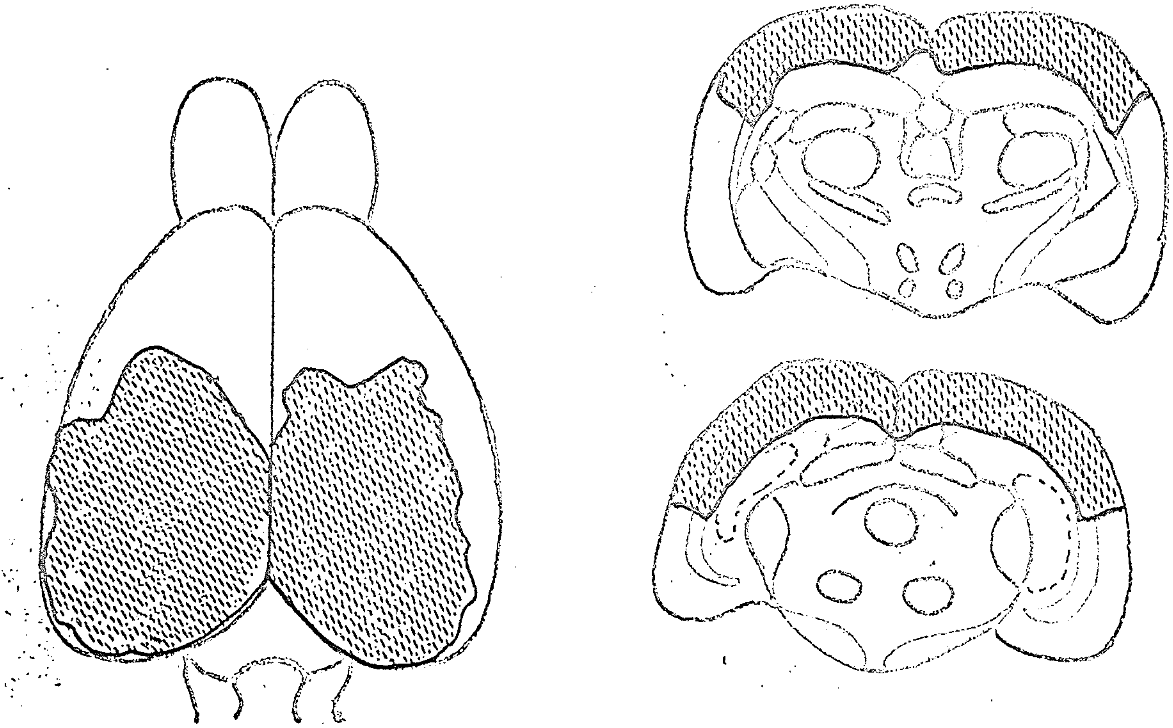

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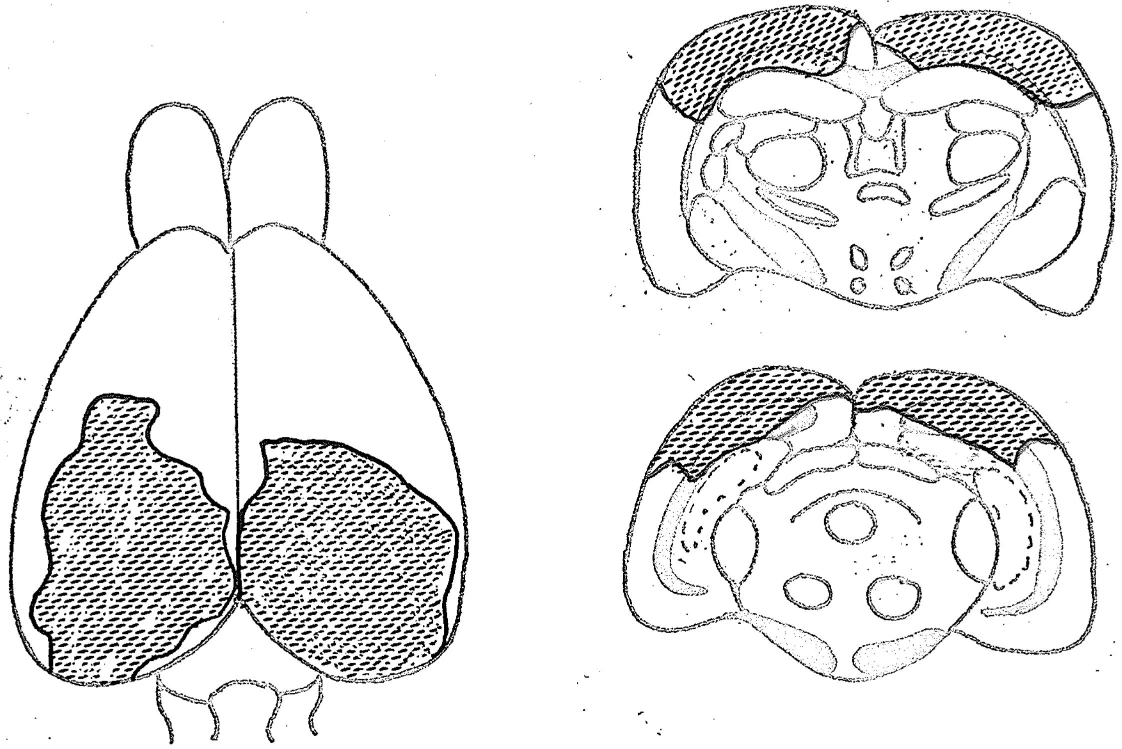

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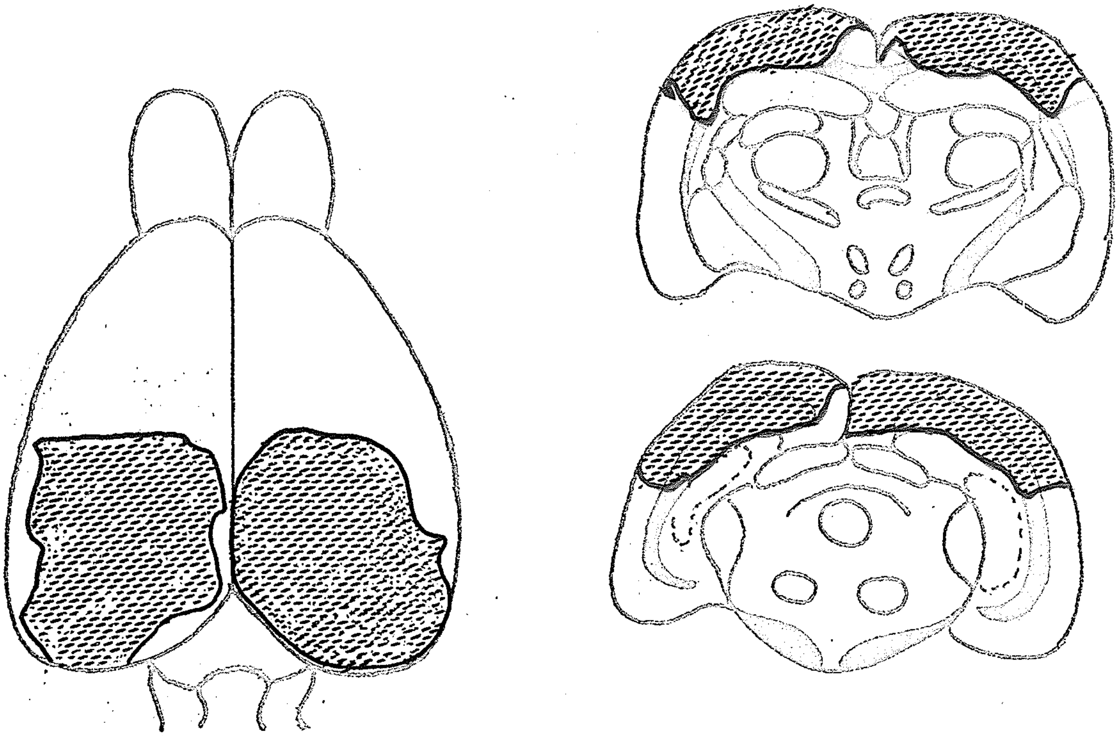

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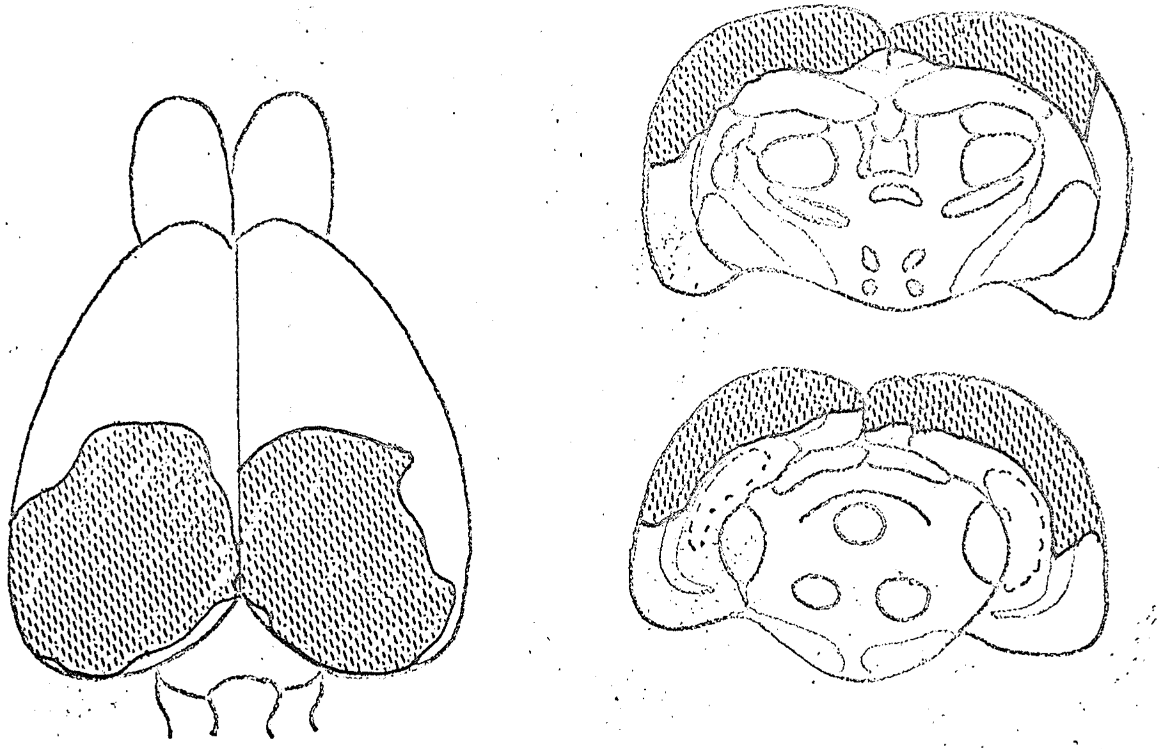

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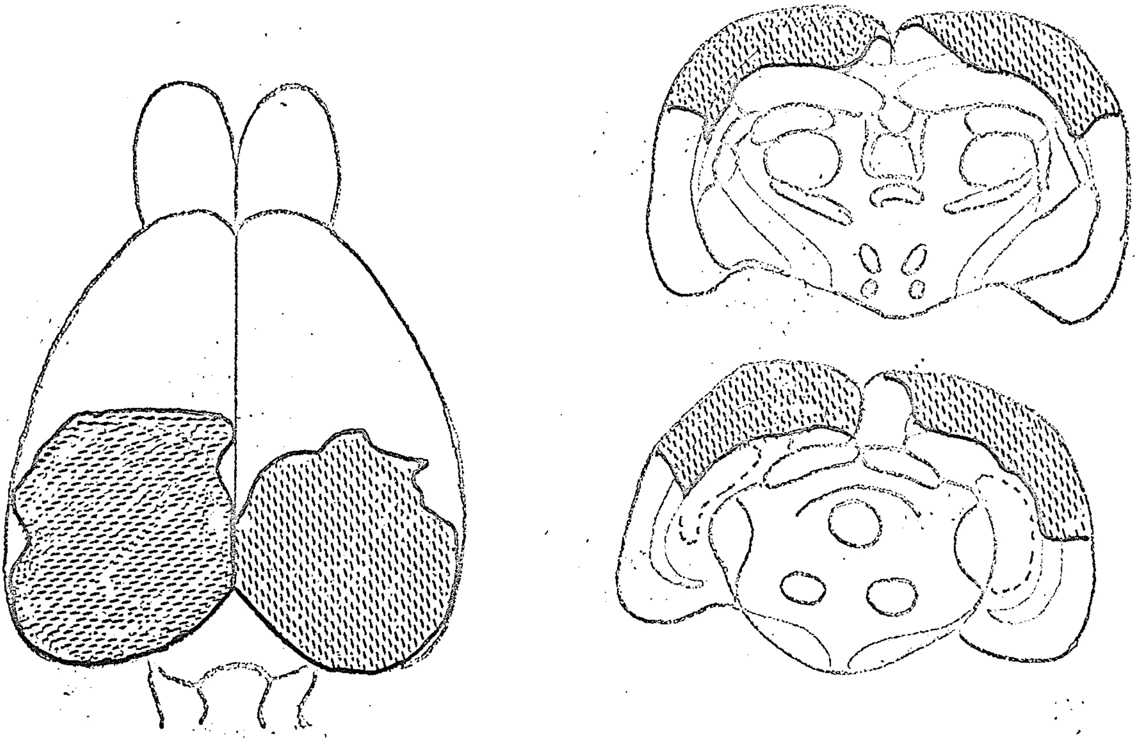

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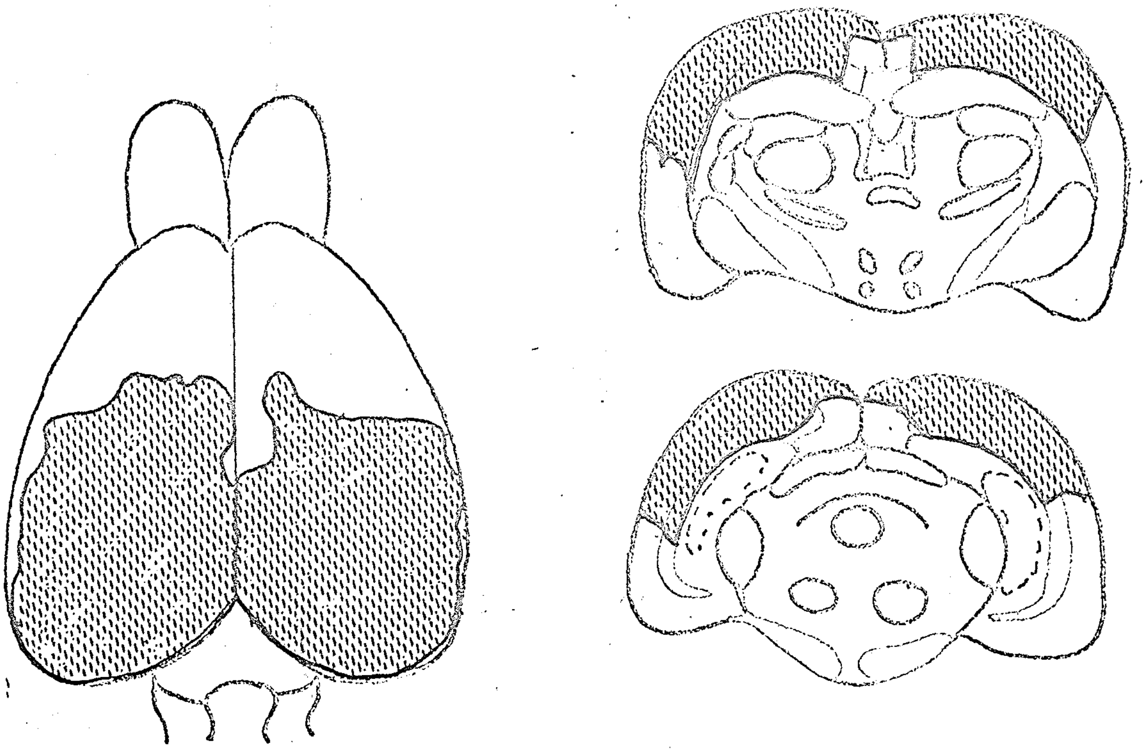

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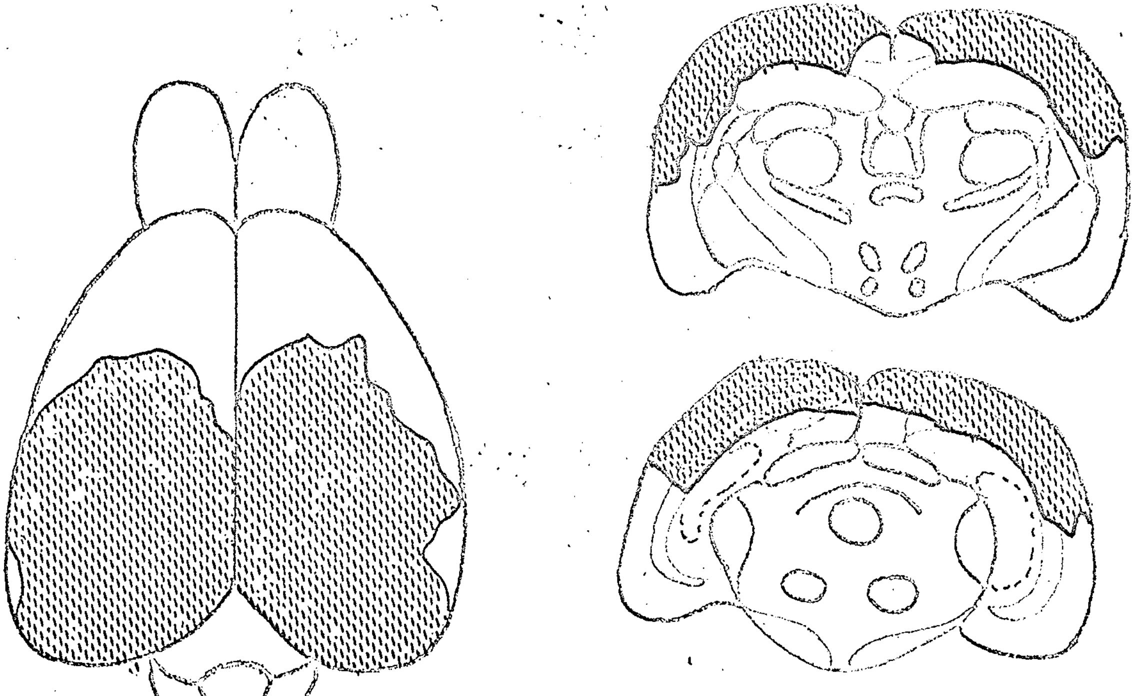

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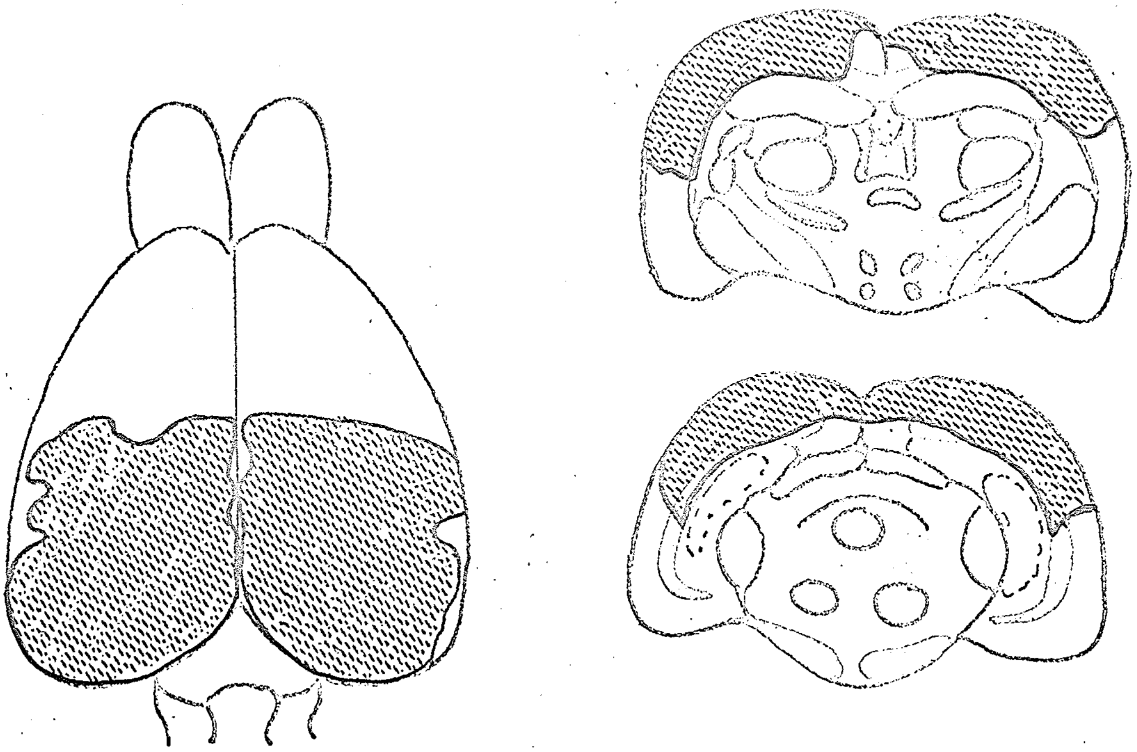

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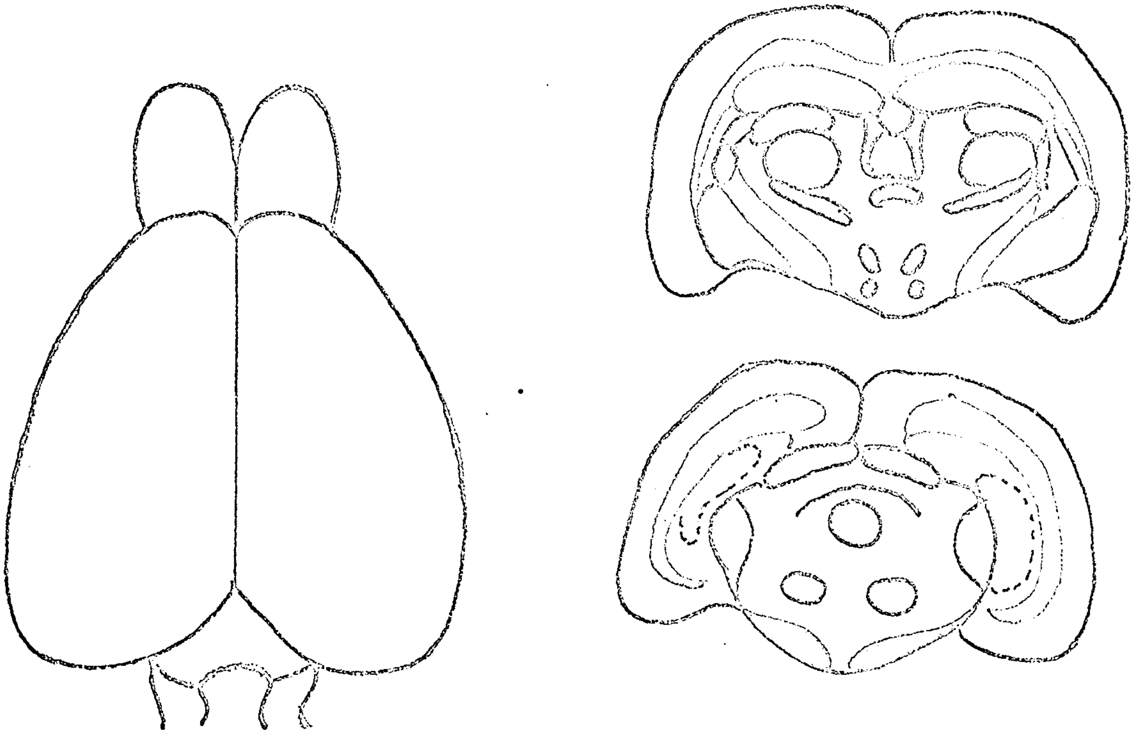

APPENDIX C

DESCRIPTION OF TRANSFORMATIONS USED IN ANALYSIS OF DATA

The kinds of transformations which were used in the analysis of the data are described in Winer (1962) pp. 218-219, and had the following form:

1) square-root transformation $X_{ijk} = \sqrt{X_{ijk}} + \sqrt{X_{ijk} + 1}$

2) logarithmic transformation $X_{ijk} = \log (X_{ijk} + 1)$.

When each of these was used it is always indicated in the text.